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Editorial Committee

Stephen Alfred Forbes

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Stephen Alfred Forbes William Trelease

Henry Baldwin Ward

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THE NASAL ORGAN IN AMPHIBIA

WITH TEN PLATES

BY

GEORGE MARSH HIGGINS

Contributions from the
Zoological Laboratory of the University of Illinois
under the direction of Henry B. Ward No. 171

THESIS

SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS

1919

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INTRODUCTION

There is considerable literature upon the development of the chondrocranium of the Amphibia, but only a little of it gives adequate details of the process of chondrification of the nasal capsule in this class of vertebrates.

Parker, in a long series of extensively illustrated papers, (1871, 1876, 1877, 1881) was the first to give any adequate account of the development of the skull in the Amphibia; but his remarks, so far as the nasal capsules are concerned, are general and no detailed description of the parts or processes of chondrification are given. Born (1877) gives, in considerable detail, the process of chondrification in *Triton cristatus;* while Stöhr (1879) who also described the chondrocranium of Triton, paid but slight attention to the ethmoidal region.

Gaupp (1893) in his well known work on the cranium of *Rana fusca* discusses four stages in the development of the skull of the frog, treating all parts with more detail than any other writer. According to Miss Platt (1897) the nasal capsule in Necturus, to a great extent, chondrifies independently of the trabeculae; but she gives but slight account of the development of the fenestrated roof of the capsules. Winslow (1898) dealt with the chondrocranium of several of the Ichthyopsida, but his account of the development of the nasal capsules has but slight detail. Peter (1898) is the only one who has described the skull of any Gymnophione; while Terry (1906), who followed the history of the nasal capsule of Amblystoma through five stages, states that the process of chondrification in Amblystoma agrees closely with that of Triton.

The work covered by this paper was undertaken with the idea of ascertaining what homologies, if any, could be drawn between the nasal capsules of the various groups of Amphibia; and to determine in how far these structures would substantiate or alter the different classifications proposed for this vertebrate group.

The work was done in the Zoological laboratory of the University of Illinois, almost entirely upon the departmental collection. It was carried on under the supervision of Professor J. S. Kingsley to whom the writer wishes to acknowledge his sincere appreciation for the many helpful suggestions and his kindly attitude during the investigation and the preparation of this paper. I wish to acknowledge my best thanks to Professor A. C. Eyclesheimer of the University of Illinois College of Medicine, for the loan of several of his series of slides of Necturus.

THE NASAL CAPSULES OF THE URODELA

AMBLYSTOMA PUNCTATUM

Amblystoma was selected as the basis of these studies upon the nasal organ of Amphibia, primarily because of the larger number of stages available, as well as on account of its intermediate position among the Urodeles. I have studied and modelled seven stages of Amblystoma, which show the successive steps, progressive and retrogressive, in the chondrification of the nasal capsule of this Urodele.

A larva 11 mm. long (Fig.1) shows but few features of a nasal capsule. The trabeculae (*t*) extend forward along the ventral margin of the forebrain and in the region of the eye, each has developed a small dorsal crest, so that in cross section it appears triangular. At this stage the trabeculae do not unite, but each expands distally into a small rhomboidal plate, the cornu trabeculae (*ct*), which supports the anterior end of the nasal organ. In a slightly older stage, a few cartilage cells appear above the medial margin of the cornu trabeculae of the left side only (Fig. 41). These cells are the beginning of a bar of cartilage, which develops along the medial dorsal margin of the nasal sac, and is known in the literature as the ethmoidal column, a term used throughout this discussion.

In a larva 20 mm. long (Fig. 2), chondrification is much more advanced. Slightly anterior to the internal nares, medial trabecular processes have united in the middle line to form a broad planum basale (*pb*), which supports the anterior end of the telencephalon. This plate is broadly concave dorsally, its lateral margins being elevated, the result of the trabecular crests. Its posterior margin is straight and at right angles to the axis of the skull, but it meets the medial margin of the trabecula in an oblique angle, because of the converging lines of the latter. The anterior margin of the planum basale passes into the expanded cornua trabeculorum, which lie in practically the same plane as do the trabeculae. The cornua extend laterally and each is concave upon its dorsal surface (Fig. 42) and supports the anterior part of the nasal organ and the organ of Jacobson; while posteriorly it reaches about the level of the middle of the planum basale where its posterior lateral angle terminates in a short caudal process. The anterolateral margin of each cornu is at about an angle of forty-five degrees to the median axis of the skull.

Dorsal and parallel to each trabecula and the median margin of the cornu of either side is an elongate rod of cartilage, the further development

of the cartilage cells above the cornu trabeculae in the earlier stage. This columna ethmoidalis (*ce*) extends posteriorly to the level of the choana, lying medial to the olfactory organ and separating it from the forebrain. As yet it is distinct from all other cartilage structures, although Terry (1906) in a similar stage has described a connection of this bar with the crista trabeculae.

In this stage is the first appearance of a cartilage roof over the nasal organ. From the posterior tip of each columna ethmoidalis, a small plate has chondrified laterally which partially covers the olfactory sac above the choana. This is the beginning of the planum tectale, which in the later stages completely covers the posterior parts of the nasal organ. In this connection it is of especial interest to note that although the columna ethmoidalis chondrifies from in front backward, the planum tectale arises at the caudal limit of the column and develops anteriorly.

In the next stage (Fig. 3), several features have been added to the capsule. The crista trabeculae (*cr t*) is well developed and has united to the posterior end of the columna ethmoidalis (*ce*), thus forming a wide trough or cavum cranii, which supports the anterior end of the telencephalon. In front of the crista, each trabecula inclines slightly toward the median line to pass into the planum basale (*pb*), which shows but slight modifications from the earlier stage.

As yet the dorsal and ventral parts of the capsule are almost entirely distinct from each other, the only connection being by the crests at the posterior end (Fig. 4). On the other hand, the columnae of the two sides are connected by a narrow ethmoidal bridge (*pe*), which lies directly above the anterior margin of the planum basale and is formed by medial processes from each ethmoidal column (Figs. 4, 44).

Between this bridge and the basal plate are procartilage cells, which in a later stage are to form, with the pons ethmoidalis, a transverse wall of cartilage (to be described later) bounding the cavum cranii in front. Up to this stage there is no complete separation between the cavum cranii and internasal space, a condition which is permanent in Urodeles like Triton.

Each columna ethmoidalis is now wider than before, except at its extreme posterior end where it joins the crista. In front of the pons ethmoidalis, each column bends obliquely outward and forward from the axis of the skull and ends at the level of the tip of the cornu. A little in front of the cristal connection of trabecula and column, each column bears a lateral process which curves down over the choana. This is the beginning of the planum tectale (*pt*) forming the posterior part of the more complete roof of the capsule in the later stage. In the literature upon the amphibian nasal capsule, this tectal plate has been called the lamina cribosa; but from its relation to the olfactory nerve it is evident that it is totally different from the cribiform plate of mammalian anatomy, hence the proposal of the name used here.

Another cartilage arises from the lateral side of each trabecula, behind the choana, and the anterior margin of the cristal connection of the trabeccula and column. This has been called by the German writers, the palatine process; but it has no relation to the palate or the palatine bone, and is better called by another name, frequently used for it, the processus antorbitalis (*pa*). It extends laterally about as far as the cornu, and is destined to form a part of the posterior wall of the nasal capsule.

As yet there are no distinct olfactory foramina, but the olfactory nerve leaves the forebrain at right angles to its median axis and passes into the capsule through the large gap between the trabecula and the column, just anterior to the crista trabeculae.

In a 34 mm. larva (Figs. 5, 6)the process of chondrification which formed the pons ethmoidalis of the 25 mm. stage, has continued ventrally and posteriorly, so that the bridge has joined the planum basale and has extended back to about the level of the planum tectale of the previous stage. The result of this is the formation of a large median wall to the cavum cranii, the only openings left being the olfactory foramina which pass into the capsules at the lateral margins of this wall. From conditions which occur in other Urodeles this median mass is best called the planum verticale, although it is much thicker than in Amphiuma and the Caecilians. As will be seen in the sequel, this planum verticale may be defined as the cartilage connecting the nasal capsules of the two sides, beginning as a median dorsal pons ethmoidalis from the two columnae and then extending down to join the planum basale. The anterior margin of the planum verticale (*pv*) is deeply excavate, and together with the medial walls of the nasal capsule, it bounds the V-shaped internasal space in which the intermaxillary glands lie. The lateral margins of the verticale slightly extend over the medial margins of the nasal organs from the olfactory foramen to the tip of the capsule, thus forming the anterior part of the planum tectale, which is pierced by a small opening (*fni*) through which the ramus nasalis internus of the fifth nerve passes into the internasal space. Thus the planum verticale is a compound structure formed from the ethmoidal bridge and the columnae ethmoidales, uniting ventrally with the planum basale.

The posterior parts of the planum tectale (*pt*), which began in the last stage (25 mm.), now forms a broad curved plate which covers the caudal half of the nasal organ, and extends forward from the crista trabeculae to the level of the anterior margin of the foramen olfactorius. Laterally it extends nearly to the level of the gap between the caudal extension of the cornu and the antorbital process; the posterior margin of the tectale is oblique, its antero-lateral margin is slightly arcuate, while in front it is produced into a small conical process (Figs. 5, 6).

The expanded cornua trabeculorum (*ct*) do not differ greatly from those of the preceding stage. The lateral margin of each cornu is slightly arcuate

and the posterior lateral angle nearly meets the lateral margin of the tectale (Fig. 5). Medially and behind, the cornu is continuous with the planum basale, which has now extended laterally so as to form a partial floor beneath the medial side of the olfactory sac. In all Urodeles the produced postero-lateral angle of the cornu supports the organ of Jacobson (vomeronasalis). This relation and also that of the organ to the lateral part of the tectale is of great aid in determining the homologies of the more complex capsule of the adult.

The antorbital process (*pa*) is now larger, forming a plate rather than a bar, and its antero-lateral angle is directed forward as a blunt process which nearly meets the posterior process of the cornu and also the lateral margin of the tectale.

In the nasal capsule of a 45 mm. larva, only a few modifications need description. The capsule (Figs. 7, 8) has not increased in length, although there has been an appreciable increase in width and depth. With the greater development of the olfactory lobes there has been a corresponding increase in the size of the cavum cranii (*cc*). The olfactory lobes extend forward only as far as the caudal third of the nasal sac, so that the olfactory foramina look obliquely forward from the antero-lateral angles of the brain case. There is a gradual change during growth in the relative positions of the nasal sac and the forebrain. In the earlier larva, brain and olfactory organs overlap for about half the length of the nasal sac, while in the adult the sensory structures are almost entirely in advance of the tip of the olfactory lobes, approximating the anuran condition.

The planum verticale (*pv*) of this stage is shorter than before but its height is almost twice that of the 34 mm. larva; so that this stage marks the beginning of the reduction of the verticale which is so much smaller in the last stage to be described.

The only other features to note in this stage are the broadening of the tectale, which process has brought the foramen for a branch of the nasalis internus on to the dorsal surface of the capsule and the extension of the antero-lateral angle of the tectale, so that it now fuses with the postero-lateral angle of the cornu, forming the first appearance of a lateral wall to the capsule. The naso-lacrimal duct passes over this connection between cornu and tectale, and empties into the olfactory sac just above the anterior end of Jacobson's organ.

Procartilage cells are abundantly distributed over the anterior end of each olfactory sac, the anterior naris being terminal in all larval stages. From these cells, the anterior cupola is formed; a process which involves the shifting of the naris to its lateral position.

In a larva near the end of metamorphosis (Fig. 9) many changes of the capsule of the early stage have occurred. The general proportions of the capsule remain unchanged, although there has been a further reduction in

the length of the planum verticale, so that one-half of the entire capsule lies anterior to this median vertical plate. The width of the verticale is also reduced by one-half to accommodate the lateral development of the olfactory organs which now lie much closer together. The anterior surface is widely concave, its dorsal margin overhanging the ventral, thus forming a partial roof over the intermaxillary glands.

The planum tectale (*pt*) now covers the entire dorsal aspect of the nasal sac and extends from the region of the choana to the tip of the capsule where it has united to the anterior margin of the cornu trabeculae, forming the cupola (Fig. 9). This area is pierced by five small foramina. Four of these are in an oblique quadrilateral, the fifth, much larger, lying behind the others. Of the four, the anterior three foramina are for the branches of the nasalis internus which are distributed to the dorsal part of the snout; while the lateral foramen passes a branch of the profundus from the capsule. The larger posterior gap contains no nervous structures and apparently is the beginning of the resorption of the cartilage roof of the capsule. The medial surface of each capsule is marked distally by a small prenasal process (*pnp*) at the base of which is the foramen nasalis internus (*fni*), above described. On the dorsal surface of the capsule is a sixth small foramen for a branch of the profundus of the fifth nerve, the result as before, of the extension of the cartilage around the nerve.

The antorbital process (*pa*) has now united to the lateral posterior margin of the tectale, a condition foreshadowed by the close association of these parts in the earlier stages, thus inclosing a large foramen between the posterior margin of the tectale and the basal part of the antorbital. This is the foramen orbito-nasalis (*fon*) into which the caudal part of the nasal sac extends, and through which the nasalis internus of the fifth nerve enters the capsule. Lateral to this foramen, the united elements of the antorbital and tectale are directed obliquely forward, covering the lateral aspect of the olfactory organ. A branch of the profundus nerve and a blood vessel pierce this plate by two foramina just posterior to its connection with the caudal extension of the cornu trabeculae (Fig. 9).

As in the earlier stages, the organ of Jacobson rests upon the caudal extension of the cornu which extends more posteriorly, and has partially united to the fused tectale and antorbital. This union of the cornu to the posterior tectale has resulted in the formation of a new foramen, the infra-conchalis of Gaupp (*fen i c*), through which the anterior part of the organ of Jacobson extends to the laterally enveloping tissue (Fig. 46, *jo*). Thus this organ rests upon a shelf formed by the cornu trabeculae, while its anterior end extends through the foramen. This infra-conchalis is separated from the large lateral narial opening by the bar, which in the 45 mm-larva connects the cornu trabeculae and the tectale. A deep groove occur-in the lateral wall of the planum tectale which leads to the posterior bound-

ary of the external naris, along which the naso-lacrimal duct passes to the olfactory organ (Fig. 45 *ld*).

This stage represents the highest development of the cartilaginous capsule in Amblystoma. The nasal organs are completely encased in cartilage, except for the external and internal narial openings. In the later stages studied, and in the early adult capsule, conspicuous gaps have formed through the process of resorption, giving way to the various membrane bones that enclose these sensory structures in the adult. That the completeness in the development of the capsule, which has been attained in this stage, is in some way associated with metamorphosis, is very evident, and it probably represents the end of the larval period.

The cartilaginous capsule of the adult Amblystoma (Fig. 10) results by reduction and specialization of structures present in the stage just described. Increase in the size of the sensory structures necessitates a capsule of enlarged dimensions, although the proportions are relatively the same. The planum verticale is reduced to a narrow bar which is relatively more posterior in respect to other capsular parts; its anterior ventral surface is deeply excavate, the dorsal surface covering the intermaxillary gland to a greater extent than before.

Strikingly characteristic of the adult cartilaginous capsule is the large five-sided gap in the roof which completely exposes the dorsal surface of the nasal organ. This gap is the result of the further resorption which just began in the last larval stage described. From its point of origin opposite the verticale in the planum tectale, resorption has extended anteriorly, laterally and posteriorly, until all that now remains of the complete cartilage roof is a slender bar of cartilage, the dorsal process of Winslow, uniting the anterior cupola with the lateral wall of the capsule. Posterior to the verticale, a narrow bar, a remnant of the ethmoidal column, passes over the foramen olfactorius and connects with the posterior tectale which now is reduced to a narrow band of cartilage. Lateral to the foramen orbitonasalis (*fon*) the tectale broadens slightly, and curving obliquely forward forms a partial roof over the choana and lateral parts of the nasal sac (Figs. 47, 48). More laterally this roof, better known as the lamina externa (*le*), is pierced by three foramina, for a blood vessel and two branches of the externus profundus nerves.

The caudal extension of the cornu trabeculae is more posterior than before, and a transverse section through the planum verticale shows the posterior end of the organ of Jacobson lying between the cornu and the lateral part of the tectale (Fig. 47). The fenestra infra-conchalis (*fen ic*) is more elongate and contains the anterior end of Jacobson's organ (Fig. 48, *jo*), which medially is partially covered by a part of the cartilage of the tectale which supports the naso-lacrimal duct. From this, a cylindrical bar of cartilage, the dorsal process, extends to the cupola, affording the only

covering to the nasal sac in this region, and which at the same time forms the medial boundary to the external naris. The small band of cartilage, which in the 45 mm. larva connected the tectale to the cornu trabeculae, persists as a flat plate separating the narial opening from the fenestra infraconchalis, and is pierced by a small foramen for the externus branch of the profundus nerve as it passes to the exterior.

Anterior to the planum verticale, a band-like cartilage, the lamina medialis (*lm*) continues forward to the cupola. It is pierced by a single large opening at the base of the prenasal process through which the nasalis internus of the profundus passes to the internasal space.

In the larva of Amblystoma there is, first, a progressive development which results in a well chondrified nasal capsule, reaching the extreme in the oldest larval stage. With the assumption of adult conditions and the more extensive development of bony structures, this capsule undergoes a marked reduction, chiefly by the resorption of parts. Evidently there is some relationship between the development of the cartilage capsule and the period of metamorphosis, the significance of which will be discussed later.

SALAMANDRA MACULATA

In a larva of *Salamandra maculata* 25 mm. long (Fig. 11), the nasal capsule has chondrified to a stage intermediate between that of the 25 mm. and 34 mm. Amblystomal larvae. The cristae trabeculorum (*cr t*) terminate abruptly just anterior to the region of the eye, from whence the trabeculae pass forward a short distance and then unite to form a broad trapezoidal planum basale (*pb*). The posterior margin of the planum is parallel to and one-half longer than the anterior, and bears a strong caudal process (*cp*), which Parker has called the hinder process, lacking in all other stages and in all Urodeles which I have studied, with the exception of a single stage of Cryptobranchus. The dorsal surface of the planum is more concave than that of the corresponding stage of Amblystoma and the ridges formed by the trabeculae are more prominent.

A broad trabecular cornu (*ct*) arises from the antero-lateral angle of the planum basale as a thin triangular cartilage, which supports the anterior part of the nasal sac. The lateral margin of each cornu is oblique to the axis of the skull and meets the posterior margin at the level of the anterior boundary of the planum basale; more medially the posterior margin curves backward and fuses with the lateral margin of the planum basale near its middle.

Parallel to each trabecula, and lying adjacent to the dorsal medial margin of each nasal sac, is the columna ethmoidalis (*ce*). In this stage of Salamandra, each ethmoidal column is united to the medial margin of the cornu, before the pons ethmoidalis appears; and this fact suggests that the columna does not arise independently here, but is a development back-

wards from the anterior cornu, just as in Spelerpes. At its posterior end a small process, the beginning of the planum tectale, extends laterally and then bends ventrally over the hinder end of the nasal sac at the level of the choana; this planum tectale arising here as in Amblystoma from an outgrowth from the columna ethmoidalis. A small groove between the anterior tip of the cornu trabeculae and the columna ethmoidalis allows for the passage of the nasalis internus branch of the profundus nerve to the internasal space (*ins*).

An antorbital process (*pa*) arises from the latero-ventral margin of each trabecula and extends laterally a short distance and anteriorly to a point in line with the caudal margin of the planum basale.

In a 38 mm. larva, the nasal capsule is similar in many ways to that of the 45 mm. Amblystoma. The capsule has doubled in size and chondrification has advanced in all parts, so that the olfactory organs are now more completely protected. Each crista trabeculae has united to the posterior end of the ethmoidal column, forming a lateral wall to the cavum cranii, interrupted only by an oval foramen olfactorius (*fo*) for the olfactory nerve.

The planum basale (*pb*) resembles that of the earlier stage, but has now completely lost the hinder process, so that the posterior margin is semicircularly excavate as in the 45 mm. Amblystoma.

In a manner similar to that of the 25 mm. Amblystoma, an ethmoidal bridge has formed uniting the columnae ethmoidales of the two sides. This represents the beginning of the planum verticale which in the later stage completely closes off the internasal space from the cavum cranii, now in continuity by means of the circular fenestra ethmoidalis (Fig. 51, *fen eth*). The dorsal surface of the rudimentary verticale is flat, continuous with the dorsal margins of the ethmoidal columns; its anterior margin bears a triangular cephalic process (*ce p*) projecting into the internasal space and partially covering the intermaxillary gland, so that a sagittal section of the verticale appears triangular.

A lateral chondrification from the entire length of the ethmoidal column now forms a broad planum tectale (*pt*), which covers the nasal organ throughout its entire length. Anteriorly the tectale has united with the tip of the cornu trabeculae, forming a complete cupola (*c*), which is continuous with the verticale and is pierced only by a single foramen for the nasalis internus of the profundus nerve. The lateral margin of the anterior part of the tectale is separated from the lateral margin of the cornu by the large oval narial opening, which lacks the deep fenestra narina of the corresponding stage of Amblystoma; but similar to Amblystoma, the posterior tectale unites by a small band of cartilage to the cornu, near its posterior prolongation, which supports the organ of Jacobson. The nasolacrimal duct passes over this bar and is formed from two branches, which come from the inner angle of the eye.

From the ventral surface of the anterior cupola (*c*), a small prenasal process arises near the foramen nasalis internus and extends downward a short distance into the enveloping tissue. The antorbital processes (*pa*) are much as before, but as yet do not meet the anterior part of the floor of the capsule.

There are some resemblances between the nasal capsules of the last larval Amblystoma (Fig. 9), and the third stage of Salamandra (Fig. 13). In both the planum basale and verticale are greatly reduced and the olfactory organs lie well anterior to the forebrain. Complete chondrification of the verticale in Salamandra has obliterated the fenestra ethmoidalis, so that internasal space and cavum cranii are no longer continuous. The anterior cephalic process (*ce p*) of the verticale is cylindrical and more elongate than before and extends forward nearly to the level of the base of the prenasal process. I have not observed this structure in any other Urodele.

Each antorbital process has grown forward beneath the lateral margin of the tectale, and has united to the caudal extension of the cornu, thus outlining two large fenestrae. Of these, the largest lies in the floor of the capsule and surrounds the choana; while the orbito-nasal foramen (*fon*) is posterior and lies between the posterior margin of the tectale and the processus antorbitalis. In this stage the lateral margin of the tectale has not united to the antorbital process, although they lie very close, so that no fenestra infra-conchalis exists; but Jacobson's organ lies between these parts as in Amblystoma.

The anterior dorsal surface of the tectale is pierced by four foramina, the medial three of which conduct rami of the nasalis internus of the profundus nerve from the capsule; its main branch passing to the foramen nasalis internus at the base of the prenasal process. The lateral and larger gap represents in Salamandra the beginning of resorption, which has been described in a corresponding stage of Amblystoma. Posteriorly the tectale is pierced by a small foramen for a branch of the profundus.

This stage of Salamandra is very similar to the last larval stage of Amblystoma, and also represents the culmination of larval development. Resorption has begun and the capsule of the adult would probably be conspicuously reduced by the growth of the covering bones. Salamandra differs from Amblystoma in the complete separation of the tectale from the antorbital, and the consequent absence of the fenestra infra-conchalis; however the approximation of these parts would suggest their connection in the adult. The ethmo-palatine of Parker is the antorbital process, and he says that in the adult it is very likely to fuse with the anterior parts of the capsule. Furthermore Parker has described in the adult the persistence of the prenasal processes and the median rostrum, and says that they seem to be the non-segmented rudiments of the paired and unpaired elements of the foremost visceral arch, whose splints are the premaxillaries. This

median rostrum is not present in any other Urodele, although prenasal processes do exist in almost all types. Parker's homologies are hardly borne out by our present knowledge.

TRITON CRISTATUS

The nasal capsule of *Triton cristatus* differs in several points from that of either Amblystoma or Salamandra. In the younger of the two larvae accessible (28 mm.), the chondrification of the capsule is far advanced and I know nothing, except by inference, of the earlier stages. At this stage (Fig. 16) the capsule is somewhat rectangular in outline, gradually tapering toward the anterior end. The cristae trabeculorum (*cr t*) are well developed and form with the trabeculae, the walls of the cavum cranii, pierced only at their anterior margins by the large circular olfactory foramina (*fo*).

Immediately in front of the crests, the trabeculae are united by a very short planum basale (*pb*), which supports the olfactory lobes and the posior part of the intermaxillary glands; the latter, in this form, extending backward beneath the anterior part of the brain. The planum basale in Triton is very much smaller than that of Amblystoma, and lies more posterior in respect to the other capsular parts. Dorsal to, and somewhat anterior to the planum basale is a bar of cartilage which unites the capsules of the two sides just in front of the olfactory foramina. This is the pons ethmoidalis (*pe*), and is developed by medial growths from the dorsal part of both capsules, much as in Amblystoma to which it bears a resemblance. Unlike Amblystoma, however, the pons is never united to the basale by the planum verticale; but throughout life it is separated from it by a large circular fenestra ethmoidalis (*fen eth*) so that internasal space and cavum cranii are separated from each other by membranous structures only.

In contrast to the larval stages of most other Urodeles, the nasal organs of Triton are almost entirely anterior to the forebrain, so that planum basale and pons ethmoidalis are close to the posterior parts of the capsule. As a result of the relation of the central nervous system to the nasal structures, each capsule appears as a segment of an elongate cone, obliquely truncate anteriorly, with the anterior half of its lateral wall interrupted by a very large narial opening. As is true for all Urodeles, the cartilage structures of each side, in front of the planum basale, are separated by an internasal space (the intermaxillary room of Born, 1877). which in Triton is more elongate and extends between the walls of the anterior two-thirds of the capsule.

Anterior to its junction with the crista trabeculae, each planum tectale (*pt*) curves outward and downward, completely covering the posterior parts of the nasal sac and the choana; laterally it continues into the lamina externa which covers the posterior part of the organ of Jacobson. More posteriorly, each lamina externa has united to the anterior prolongation of

the antorbital process, thus completing the foramen orbito-nasalis (*fon*) through which the nerves of the nasal region enter the capsule. A small foramen in the tectale, just opposite the pons ethmoidalis conducts a branch of the profundus nerve from the capsule; while the larger oval gap in the anterior tectale, separated from the external naris by a narrow bar is one of the gaps described by Born in the adult.

The lamina medialis (*lm*) forms the medial wall of the capsule, anterior to the foramen olfactorius, and is continuous with the tectale and the cornu trabeculae (Fig. 56), thus bounding the internasal space. The floor of the capsule is formed by a large trapezoidal cornu trabeculae which extends back to the level of the pons ethmoidalis where it forms the anterior margin of the choana. Its lateral margin unites to the lamina externa, forming the boundary to the naris, over which the naso-lacrimal duct passes to the nasal sac, as in Amblystoma and Salamandra. Posterior to its junction with the lamina externa, each cornu terminates in a small posteriorly-directed process, which supports the organ of Jacobson; although, as in Salamandra, a fenestra infra conchalis does not yet exist. At the anterior end, the floors of the two capsules approach each other, and at the extreme medial tip of each is a small prenasal process (*pnp*), probably the homologue of that structure in both Amblystoma and Salamandra. The nasalis internus of the profundus nerve leaves the capsule through the foramen at the base of the prenasal process.

The nasal capsule of the older larva of *Triton cristatus* (35 mm. long) is intermediate between the 28 mm. stage and that described by Born (1877), in which large gaps have developed. In this stage there has been a reduction in the length of the capsule, most of which occurs at the anterior end, so that the width is greater in proportion to the length than in the earlier larva. The relation of the forebrain to the nasal sac is much as before; but in the adult, according to Born, all olfactory structures are entirely anterior to the central nervous system. The planum basale and the pons ethmoidalis are much as in the earlier stage, except that the pons is now much farther anterior than is the basale, while the foramen olfactorius and ethmoidalis are larger than before (Fig. 17).

Cartilage has formed around the branch of the profundus nerve which supplies the organ of Jacobson, cutting off a smaller foramen adjacent to the foramen orbito-nasalis (Fig. 17, 57). Just anterior, and slightly lateral to this foramen, the lamina externa has united to the caudal extension of the cornu trabeculae thus outlining the foramen infra-conchalis, as in Amblystoma, through which the organ of Jacobson protrudes from the capsule.

Further description of this capsule is unnecessary, with the exception of the cupola (*c*), which now encloses the anterior parts of the nasal sac, so that now the external naris is entirely lateral. The lamina medialis (*lm*)

is pierced by a small foramen for a branch of the nasalis internus of the profundus nerve, the main part of which leaves the capsule through the foramen in front of, and at the base of the prenasal process. At the anterior end of the floor of the capsule is a small gap which I believe to be the beginning of the larger gap described by Born for the adult.

It is impossible to be certain of all the homologies between the nasal capsule of Triton and that of Amblystoma, without the early stages. Born (1877) has described the process of chondrification, but has shown no figures for his early stages. Terry (1906) says: "The development of the cartilaginous nasal skeleton of Amblystoma is comparable in many respects with the processes in Triton as described by Born." Born says nothing of an ethmoidal column which chondrifies independently and then later becomes associated with the trabecula; on the contrary he says: "Bei den Tritonen die Knorpelkapseln der Nasenhöhlen durch directes auswachsen der Trabecel gebildet werden." The lamina medialis, planum tectale and lamina externa would thus be formed by a continuous growth from the trabecula; while the many gaps in the capsule would arise by interruptions in the process.

Throughout its development, Amblystoma never has a fenestra ethmoidalis completely outlined, and yet it is distinctly present in both stages of Triton; and Born says: "Dieser Internasalraum ist bei Triton cristatus und taeniatus, niemals durch eine knorpelige Wand von der Schädelhöhle geschieden, sondern immer hautig gegen dieselbe abgeschlossen."

In larvae of Salamandra, Pelobates and Rana, the fenestra ethmoidalis is complete, being bounded by cartilage upon all sides, but is closed in the adult; while it persists throughout life in Triton and Diemictylus.

DIEMICTYLUS VIRIDESCENS

The nasal capsule of a 38 mm. larva of *Diemictylus viridescens* resembles in many ways that of the 35 mm. *Triton cristatus*. In both, the two capsules are united by a very small planum basale, the only connection between them even in the adult Diemictylus, which lacks the pons ethmoidalis; so that internasal space and cavum cranii are continuous cavities. The small planum basale (*pb*) supports the anterior part of the telencephalon which reaches forward into the internasal space; so that olfactory lobes and intermaxillary glands overlap in this animal (Figs. 14, 53).

The antorbital process (*pa*) has united to the posterior margin of the tectale at two places, thus outlining two small fenestrae the inner of which is the foramen orbito-nasalis (*f o n*) for the nasalis internus of the profundus nerve; while the outer conducts the externus branch of the profundus, which supplies Jacobson's organ.

Anterior to these foramina, the united elements of the planum tectale and the antorbital process completely cover the dorsal and lateral parts of

the olfactory organ; and together with the posterior prolongation of the cornu form a shelf upon which the posterior parts of Jacobson's organ rest. Slightly anterior to its junction with the cornu, the tectale is pierced by a small circular foramen, which, like the infra-conchalis of Amblystoma and Triton, contains the anterior end of the organ of Jacobson. The planum tectale is interrupted on its anterior half by two oval openings, of which the external naris is the larger, extending back nearly to the middle of the capsule. The more medial gap is much smaller and marks the beginning of the process of resorption, just as in the older Triton larva.

The lamina medialis (*lm*) is continuous with the tectale and forms the medial wall of the capsule from the planum basale to the anterior cupola; while ventrally, it curves into the floor of the capsule which is pierced by two small foramina, through which rami of the nasalis internus nerve leave the capsule. The main branch of this nerve passes to the internasal space through the larger foramen just in front of the base of the pre-nasal process.

The adult Diemictylus (Fig. 15) shows no further chondrification of structures than those present in the larva. Ossification has taken place in all parts and further resorption has increased the size of the gaps present in the earlier stage. A single foramen exists above the antorbital process, so that both nasalis internus and externus of the profundus nerve enter the capsule through the foramen orbito-nasalis.

The planum tectale is more vaulted than before, and its posterior half is pierced by two foramina; the medial of which is for a branch of the profundus nerve, while the lateral and larger one contains, as before, the cephalic end of Jacobson's organ. The anterior tectale has two large openings, the external naris, lateral in position, and, medial to this, the further development of the gap begun by resorptive processes of the larva.

The ventral surface of the adult capsule has a greatly enlarged choana, which occupies the posterior two-thirds of the floor. It is bounded laterally by the prolongation of the cornu, which in this stage extends beyond the junction to the tectale, so that a short process, behind the shelf, supports the posterior parts of the organ of Jacobson. The anterior part of the floor and the cupola need no description, further than the mention of five small foramina for branches of the nasalis internus nerve.

The nasal capsules of Triton and Diemictylus are very close. The presence of the same large gaps, and the reduced planum basale, together with the continuity of cavum cranii with the internasal space are strong resemblances between the two. The fenestra ethmoidalis is not a permanent character of any other adult, although it is temporary in some larvae as Salamandra and certain Anura. There are some resemblances between the capsules of the adult Amblystoma and Diemictylus. In both, the anterior part of the organ of Jacobson extends through a foramen which in

Amblystoma is called the infra-conchalis, separated from the naris by a cartilage bar; while the posterior part of Jacobson's organ rests upon a shelf formed by the prolongation of the cornu. The orbito-nasal foramen, the choanal opening, and the relation of the olfactory organ to the capsule, are features common to both Amblystoma and Diemictylus; and yet the absence of a planum verticale, the greatly reduced planum basale and the complete continuity of internasal space with cavum cranii in the latter form, preclude the determination of close relationships here.

CRYPTOBRANCHUS ALLEGHANIENSIS

Practically no work has been done upon the development of the skeleton in the larval stages of Cryptobranchus, although the adult skull and nasal structures have been described by Parker (1876), Wiedersheim (1877), and Wilder (1892). I have studied four stages in the chondrification of the nasal capsule, and although my material lacks some intermediate steps in the process, yet I am able to recognize the method of development and to note some features that may prove interesting from a phylogenetic point of view.

The early process of chondrification in Cryptobranchus is similar to that in Amblystoma, and my earliest stage suggests the eleven mm. larva of that animal with certain additional features. In a larval Cryptobranchus two weeks after hatching (Fig. 22), a nasal capsule has not yet formed. The cristae trabeculorum (*cr t*) are very strong and high, but terminate abruptly near the anterior margin of the eye; while the trabeculae continue anteriorly, turning slightly medially but not meeting to form the planum basale. Each is curved upon its medial surface, which rests against the olfactory lobe; while anteriorly a ventral lateral expansion of the trabecula is the beginning of the cornu (*ct*), which resembles Amblystoma, and ends in a blunt process in the surrounding tissue.

In contrast to the eleven mm. Amblystomal larva, trabecular crests are well developed in this stage of Cryptobranchus; while on the other hand, the cornua trabeculorum which are well developed in the young Amblystoma are just beginning to chondrify in Cryptobranchus. Antorbital processes have not formed, nor is there any trace of an ethmoidal column as in the youngest Amblystoma.

In a larva five weeks after hatching (Fig. 23), chondrification has advanced in all parts, but the absence of an intermediate stage prevents a definite conclusion as to the origin of certain structures. In general the capsule resembles in many respects that of the 25 mm. Salamandra.

From the anterior end of the crista, each trabecula inclines toward the median line for a short distance, and then passes straight forward and is united with its mate by a small planum basale (*pb*) similar in size to that in *Triton cristatus*. This planum basale differs from that of any Urodele thus

far described, in the fact that the dorsal surface is not concave but is convex and bears upon its anterior half a distinct median swelling which probably is the beginning of a planum verticale (Fig. 58). The anterior surface is straight and at right angles to the median surface of the skull, while the posterior possesses a short caudal process similar to that in the 25 mm. Salamandra larva.

Anterior to the planum basale, each trabecula extends forward a short distance and from its medial margin a columna ethmoidalis (*ce*) arises dorsally as a broad band of cartilage, partially separating the anterior part of the nasal sac from the internasal space. Passing backwards, upwards and outwards along the dorsal medial side of the olfactory organ, each column becomes more rod-like; and at the level of the anterior margin of the planum basale it expands into a large rhomboidal plate, the planum tectale (*pt*) which extends forwards and outwards, covering the dorsal and lateral parts of the nasal sac. Each tectale is pierced by a small foramen through which a branch of the profundus nerve passes from the capsule. Posterior to the tectale, each column continues backward and unites to the crista trabeculae.

The cornu trabeculae (*ct*) of Cryptobranchus differs from that of any other Urodele. In contrast to the board triangular plate of both Amblystoma and Salamandra, it is reduced to a narrow bar, which curves backwards and upwards from the lateral anterior margin of the trabecula to a point just below the tectale, to which it fuses in a later stage. A small notch at the anterior end of the capsule, between the ethmoidal column and the cornu allows for the passage of the nasalis internus nerve to the internasal space.

From each trabecula, just posterior to the large foramen olfactorius, a slender process passes laterally a distance equal to the width of the trabecula, and then bends abruptly to pass backward to the pterygo-quadrate, while it utterly lacks any anterior prolongation. The morphological relations of this bar will be discussed in connection with a later stage.

In a larva two months after hatching, a more complete capsule has formed. The planum basale has lost the hinder process and is now continuous with the planum verticale, which unites the two capsules just anterior to the oval olfactory foramina and completely separates the cavum cranii from the internasal space. Anterior to the verticale, the columna ethmoidalis and cornu trabeculae have expanded to form the lamina medialis covering the entire medial surface of the nasal organ. A notch, marking the junction of column and cornu, allows for the passage of a branch of the nasalis internus to the internasal space.

The planum tectale is considerably larger than before, reaching back to the crista and extending forward over the posterior tip of the cornu trabeculae, with which it is not yet united. It is pierced by a small foramen as

in the earlier stage. A wide bay, the fenestra narina, marks the anterior boundary of the tectale, and here, as in Amblystoma, is a larval character, disappearing in the adult. The cornu trabeculae is somewhat wider than before, although differing considerably from the broader cornua of other Urodeles. A small notch at the anterior end of the cornu conducts a second branch of the nasalis internus from the capsule.

In the last stage of Cryptobranchus studied, a larva three months old (Fig. 24), chondrification has advanced in all parts, forming a well-defined nasal capsule, resembling in some respects the 45 mm. Amblystoma. The planum basale and verticale are much as before, supporting the olfactory lobes, and uniting the capsules of the two sides just anterior to the olfactory foramina. Anterior to the planum verticale, the lamina medialis (*lm*) formed by both ethmoidal column and trabecula, together with the cornu forms the anterior cupola of the capsule, which is pierced by two foramina, one medial and the other ventral, through which the branches of the nasalis internus nerve leave the capsule. The olfactory duct continues forward beyond the lateral margin of the cupola and opens through the external naris, anterior to all capsular structures.

The cornu trabeculae is much as in the earlier stage, except that it has now united to the anterior extension of the planum tectale, just as in all other Urodeles thus far described; and the organ of Jacobson rests upon the caudal extension of the cornu behind this connection. The tectale itself is larger than before, reaching forward a short distance beyond its junction with the cornu, thus completely covering the choana and the dorsal parts of the nasal sac. The fenestra narina is deeper than before, extending back from the naris to the planum verticale. A branch of the superficialis nerve enters and leaves the capsule through this bay; but in a later stage, cartilage has chondrified around these nerves leaving two small foramina, and completely obliterating the narina, as in the last larval stage of Amblystoma.

In this stage, the bar of cartilage mentioned in connection wth the five weeks larva as extending at right angles from the side of the trabecula, has attained such relations as to throw light upon its morphology. At its tip it is directly connected with the anterior end of the pterygoquadrate bar, which extends back to the otic region where the relations are much the same as in all Urodeles. This completeness of connection of the pterygoquadrate with the anterior parts of the trabecula is paralleled, so far as I know, only in the Siberian genus Ranodon (Wiedersheim 1877, Fig. 69), and is lost in the adult of Cryptobranchus, both our species and the Japanese japonicus.

Some years ago, Gaupp questioned a statement by Kingsley (1892, p. 672), who said: "the lower process may retain the name 'antorbital', usually applied to it, for Amphiuma presents no evidence that it is the

palatine cartilage as Gaupp interprets it." Gaupp (1893, footnote p. 430) says: "Hierzu möchte ich bemerken, dass ich die beiden Namen 'Antorbital-fortsatz' und 'Cartilago palatina' durchaus für dasselbe Gebilde gebraucht habe (17, p. 115: 'die Cartilago palatina' oder wie die englischen Autoren Huxley und Parker den Knorpel nennen, den 'Processus antorbitalis'). Als 'Processus palatinus' wird der Knorpel aber z.B. von Friedreich und Gegenbaur bezeichnet (14, p. 29), auch Hertwig (24) nennt ihn auf den Figuren 'Cartilago palatina' (C.p.), und Wiedersheim (58, p. 483) spricht von einen Antorbitalfortsatz oder 'Gaumenfortsatz' der deutschen Autoren. Da ich beide Bezeichnungen in der Literatur vorfand, so erwähnte ich sie auch beide, habe aber nicht etwa einem bekannten Gebilde eine neue Deutung geben wollen. Kingsley scheint unter 'Palatine cartilage' hier etwas Besonderes zu verstehen; was das ist, kann ich aus seinen Angaben nicht ersehen."

Winslow (1898) discussed the question, and concluded that until it was shown that the process in Urodeles arising from the trabecula in front of the orbit was actually a part of the pterygoquadrate the name antorbital should be retained. A further point is that the term palatine cartilage is misleading, implying that it is the rudiment of the palatine bone, which is not cartilaginous in origin.

With the evidence now presented by Cryptobranchus, it would seem as if the basal part of the process here, and by implication in all Urodeles, is really an anterior prolongation of the pterygoquadrate. But the anterior portion of this process is something additional, and although possibly pterygoidal in origin, may retain the name antorbital. Then in all other groups, where the posterior connection to the quadrate is lost, the entire outgrowth, although partly pterygoidal, is best known as the antorbital process. Of course this retention of the anterior part of the pterygoid in both Cryptobranchus and Ranodon larvae is an ancestral feature lost elsewhere among the Urodeles. As stated in the above, the adults of both species of Cryptobranchus have lost the connection of the pterygoid with the side of the cranial wall, and in both the direction of the posterior plainly pterygoidal part of the cartilage would not suggest that in the larva there was any such connection with the trabecula or any relation with the palatine bone.

Of the Urodeles thus far described, Cryptobranchus stands alone in the origin of the planum verticale, which arises as a medial dorsal growth from the planum basale, subsequently uniting to the medial margins of the columnae ethmoidales and closing off the cavum cranii from the internasal space. Thus at no time does a pons ethmoidalis or a fenestra ethmoidalis exist in Cryptobranchus, like that in Amblystoma and Salamandra. On the other hand the columna ethmoidalis in Cryptobranchus recalls that structure in Salamandra which, arising in both from the medial margin of

the cornu, grows posteriorly along the nasal sac. Unlike Salamandra, however, the planum tectale does not develop from the posterior end of the ethmoidal column, but rather chondrifies laterally from about its middle.

Although the planum tectale and the anterior cupola of my later stage resembles in some ways those of both Salamandra and Amblystoma yet the large planum basale and cornu trabeculae of the latter forms, do not exist at any time in Cryptobranchus, both of these structures being greatly reduced.

SPELERPES BILINEATUS

The nasal capsule of a Spelerpes larva 15 mm. long (Fig. 18) differs but little from those of the early stages of all Urodeles. The trabeculae (*t*) are more cylindrical than in Amblystoma, however, and extend forward to the tip of the forebrain, not meeting as yet to form the planum basale. At their anterior ends, each trabecula expands into a triangular cornu, considerably smaller than the cornua of corresponding stages of Amblystoma, and, which only partially supports the anterior part of the nasal organ (Fig. 59). Ethmoidal column nor crista trabeculae have not appeared in this stage.

In a 37 mm. larva (Fig. 19) other parts of the capsule have chondrified, but on the whole the capsule is far more simple than any other Urodele of that age. The cristae trabeculorum (*cr t*) are well developed and together with the trabeculae form the walls of the cavum cranii. Each crista terminates at the level of the antorbital process, and from its dorsal margin a short process extends anteriorly, which appears to be associated with the development of the ethmoidal column, as described in the later stage.

From its junction with the crista, each trabecula inclines toward the median line and is united with its mate by a small planum basale (*pb*), convex upon its dorsal surface and resembling this structure in the second stage of Cryptobranchus. Just anterior to the planum basale the trabeculae are strongly concave and a prominent ridge has developed along their medial margins, forming a groove for the branches of the nasalis internus of the profundus nerve (Fig. 60). The trabecular cornu is well developed in this stage; its posterior margin extending backwards as a short process to the level of the anterior margin of the planum basale.

The antorbital processes (*pa*) are much as in others of the order, arising from the trabecula just beneath the crista, extending laterally a short distance, and then bending anteriorly toward the capsule.

My oldest stage of Spelerpes is a larva 46 mm. long (Fig. 20). Some additional structures are present, but the capsule is not completely developed and satisfactory comparisons with the capsules of other Urodeles can not be made.

Opposite the eye, the cristae trabeculorum (*cr t*) are low; but farther forwards they are higher, their anterior ends being free from the lower

trabecula and reaching farther forward than before (Fig. 21). Anterior to the crista, each trabecula turns more abruptly toward the median line for a short distance, and then anteriorly; uniting by a very small planum basale, which in this stage is flat and level, with the dorsal surfaces of the trabeculae.

Anterior to the planum basale, the trabeculae continue forward, separated from each other by a narrow internasal space; each expands distally into a small cornu which supports the tip of the nasal organ. Arising from the dorsal and medial margin of each trabecula, just anterior to the planum basale, is a small process which extends backward a short distance along the medial margin of the nasal sac. This process is the further development of the medial ridge of the trabecula in the 37 mm. stage; and from its relation to the nasal organ, it must be the beginning of the columna ethmoidalis, whose further history is unknown (Fig. 61).

I regret that I have no older stages showing the farther chondrification of the capsule; thus preventing a careful comparison with other Urodeles. In general, however, Spelerpes seems to indicate a retarded growth in all parts. In corresponding ages of other Urodeles, there is a much more complete capsule than in Spelerpes.

I have not observed the free anterior extension of the crista in any other Urodele, with the exception of Amphiuma; and judging from its relation to the nasal organ and trabecula, it would appear as though this process is the posterior beginning of the ethmoidal column. In other words the columna ethmoidalis in Spelerpes may arise by the fusion of two parts independent of each other; the anterior part from the medial margin of the cornu, the posterior part from the anterior margin of the crista. In no other Urodele, as far as I have seen, does the column arise in just this way; however the early development of the crista trabeculae in Cryptobranchus and the lateral development of the tectale from the middle of the ethmoidal column, leads me to conclude that in Cryptobranchus the column arises, as in Spelerpes, from two distinct independent outgrowths.

The small planum basale is similar to that in Cryptobranchus, but the larger cornu in the 37 mm. stage is more like that of Amblystoma. My material does not show the formation of the planum verticale, but it evidently does not arise as a dorsal growth from the planum basale, but more probably by medial growths from the ethmoidal columns; thus in this particular, approaching the condition in Salamandra.

The complete absence of intermaxillary glands, the close approximation of the capsules anterior to the planum basale, as well as the small size of the latter, are points of similarity to Cryptobranchus, which, on the evidence of larval characters alone, I believe Spelerpes more closely resembles.

PLETHODON ERYTHRONOTUS

Winslow (1898) has described the nasal capsule of a 20 mm. larva of *Plethodon glutinosus*, and he compares it with a 45 mm. Amblystoma. I have not studied any larval form of this genus, but have examined and modelled the capsule of an adult, which is similar in many respects to my last stage of Amblystoma. In the adult, ossification is extensive and in some parts, all traces of a chondrocranium have disappeared. This is especially true in the region of the eye, where the trabecular crests have disappeared as far forward as the olfactory foramina, so that these openings are confluent with the foramina orbito-nasales in this stage (Fig. 27).

The dorsal surface of the nasal organ is exposed throughout its entire length by a large gap in the capsule, similar to that of the adult Amblystoma; so that the planum tectale is reduced to a small cartilage plate covering the posterior end of the nasal sac behind the choana. The lamina externa (*le*) formed by elements of the tectale and processus antorbitalis, passes obliquely forward as a band of cartilage, protecting the lateral parts of the nasal sac and the organ of Jacobson (Fig. 62). The nasalis externus of the profundus nerve enters the capsule through a small foramen in this plate, and is partly distributed to Jacobson's organ; while the main branch of the nerve leaves the capsule through the foramen in the more anterior part of the capsule. Just lateral to the foramen nasalis externus (*fne*), the lamina externa abruptly expands from its ventral margin into a horizontal plate which partly covers Jacobson's organ, its lateral angle terminating in a small anterior process; while more anteriorly it narrows considerably and lies directly above the posterior prolongation of the cornu (Fig. 63). The anterior medial angle of the lamina externa is united by a cylindrical bar to the anterior cupola, as in the adult Amblystoma (Fig. 10), which separates the external naris from the large gap in the dorsal surface. The naso-lacrimal duct passes to the nasal organ through the notch between this bar and the anterior part of the externa, which is pierced by the foramen for the exit of the nasalis externus, as mentioned above.

The floor of the capsule is formed by the cornu trabeculae, which has united to the lateral margin of the lamina externa, and continues posteriorly as a short process supporting the anterior end of the organ of Jacobson. The ventral gap in the capsule is very large and is similar to that in Amblystoma.

The planum basale and verticale are united throughout their entire length, forming a thick plate which unites the capsules just anterior to the olfactory foramina and separates the internasal space from the cavum cranii. Anterior to these parts, the lamina medialis (*lm*) forms the medial wall of the capsule; narrower at its junction to the verticale, it becomes wider more anteriorly and finally uniting with the cornu trabeculae, it forms the anterior vault of the capsule. Midway between the tip of the capsule

and the verticale, the lamina medialis is pierced by two foramina, through the dorsal of which, the nasalis internus of the profundus nerve passes to the intermaxillary gland; while a blood vessel passes through the more ventral one. A small prenasal process extends anteriorly a short distance from the median ventral surface of the cupola. The internasal space is deep and narrow, and it is filled with intermaxillary glands which extend back beneath the planum basale, to its posterior margin. In the presence of these glands, Plethodon differs from Cryptobranchus and Spelerpes but resembles Amblystoma and Salamandra.

In all essentials Plethodon resembles very closely the adult Amblystoma to which it is probably nearly related. The absence of earlier stages has prevented a study of the development of the capsule; but comparing the single larval stage of Winslow with my early stages of Amblystoma, coupled with the many resemblances between the adults, I am inclined to place Plethodon very near to Amblystoma. The absence of the fenestra infra-conchalis in Plethodon is the primary difference between these capsules; but the position and size of the planum verticale, the lamina externa and medialis, the anterior cupola as well as the large dorsal and ventral gaps are resemblances that suggest a very close relationship between these animals.

NECTURUS MACULATUS

As in Spelerpes, the chondrification of the nasal capsule of Necturus is greatly retarded; so that, except for the mere extension of the trabeculae into the head region, there is no evidence of a nasal skeleton up to the 25 mm. stage. In higher Urodeles of this size, well developed capsules are already chondrified.

In a 24 mm. larva, the trabecular crests are not developed, and the cylindrical trabeculae incline toward each other, but do not unite to form the planum basale. There is no evidence of a cornu at the anterior end, nor has the antorbital process yet chondrified; but procartilage cells have formed near the trabecula which indicate its later development. The forebrain lies lateral to the nasal sac and extends slightly anterior to the trabeculae.

In a slightly older stage (Fig. 25), the anterior ends of the trabeculae more closely approach each other and near the tips they have expanded dorso-laterally, so that a cross section of the trabecula in this region is reniform. Miss Platt (1897) has described the independent chondrification of the planum basale, and its subsequent connection to the trabecula; although this stage does not show the chondrified basale, yet a few procartilage cells lying in the tissue between the anterior ends of the trabeculae indicate its origin as independent of the trabeculae. In this stage also, a small triangular antorbital process has chondrified from the trabecula.

In a 30 mm. larva (Fig. 26), some additional structures are present, although the capsule differs considerably from any other Urodele. The trabeculae are now united near their anterior ends by a planum basale (*pb*), trapezoidal in outline, its posterior margin being one and one-half times the length of the anterior. A median swelling upon the dorsal surface of the planum basale, together with the trabecular thickenings give the plate a bi-concave appearance, the olfactory lobes resting in the concavities. This median swelling, more evident over the anterior half of the planum and which resembles a similar structure in Cryptobranchus, must be regarded as a rudimentary planum verticale, although the later stage shows no further development of it (Fig. 64). Anterior to the planum basale, the trabeculae continue forward a short distance; and, without expanding into cornua so typical of other Urodeles, each trabecula, separated from its mate by a wide internasal space, ends bluntly in the surrounding tissue.

The beginning of the well-known fenestrated capsule of the adult Necturus, covering the nasal organs, mentioned and figured by Wiedersheim (1877) and others, appears in this stage. Directly over the medial margin of the nasal sac, and some distance from the trabecula is a small bar of cartilage, the columna ethmoidalis (*ce*), which extends from a little in front of the level of the anterior end of the trabecula back to the level of the posterior margin of the planum basale. At no time is it united to the trabeculae, and it recalls in origin and position this column in Amblystoma. A more posterior extension of this bar in the 33 mm. and 35 mm. stages, in which it reaches nearly to the antorbital process, suggests that here, as throughout the order, this bar chondrifies, first in the anterior parts and then develops posteriorly; although here it never unites to a crista trabecula, a structure entirely lacking in Necturus. Also in the 33 mm. and 35 mm. larvae I have observed cartilage cells along the lateral margin of the nasal sac, some of which lie between the folds of the nasal epithelium. These several areas do not seem to arise as a continuum, but chondrify independently and later become connected to each other and to the ethmoidal column to form the roof of the fenestrated capsule.

The antorbital processes are now more like those of other Urodeles, reaching forward a short distance toward the other parts of the capsule.

In the last stage of Necturus studied, a larva 45 mm. long (Fig. 28), the fenestrated nasal capsule (*fen pr*) has developed and resembles that of the adult. The trabecula (*t*), planum basale, and anterior extensions of the trabeculae are much as before, differing only in size; while the planum verticale, earlier prominent as the median ridge on the basale, is now reduced to a small swelling on the anterior half of the basal plate. Accordingly, the posterior half of the basale, which supports the olfactory lobes, is slightly and broadly concave.

The entire dorsal surface of the simple nasal sac and part of the lateral surface is covered by a curved and fenestrated cartilage, more extensive posteriorly where it curves ventrally over the choana. This process is a further development from the columna ethmoidalis with large additions from the cartilage cells described in the earlier stage, which now have united to each other in such a way that small gaps expose the dorsal surface of the nasal sac (Fig. 65). In front, the lateral parts of the fenestrated process are lacking, so that the ethmoidal column alone forms the roof in this region; while the more extensive chondrification occurs in the posterior parts. This more complete development posteriorly, and the gradual reduction toward the anterior end culminating in the unspecialized ethmoidal column, indicates a development from behind forwards, and recalls the condition in both Salamandra and Amblystoma in which the columna ethmoidalis develops lateral processes, first from its posterior parts. Although the fenestrated process of Necturus never unites to other capsular parts, yet because of its relation to the ethmoidal column and the nasal organ, it is the homologue of the planum tectale of other Urodeles.

The antorbital processes (*pa*) are larger than before, and although they lie near the lateral parts of the fenestrated tectale, the two never unite, so that a foramen orbito-nasalis is never completely enclosed; nor is there any circumscribed olfactory foramen since the column is completely distinct from the trabecula, and the olfactory nerve passes between column and trabecula to the olfactory organ.

The early development of the nasal capsule of Necturus resembles that of other Urodeles to this extent; the trabeculae with their antorbital processes, the planum basale and the ethmoidal columns are common to all. On the other hand, Necturus lacks the characteristic expanded cornua, the trabeculae ending bluntly, as well as a planum verticale and lamina medialis, which in all other Urodeles completely separates the nasal organs from each other and closes the internasal space from the cavity of the forebrain. The nasal organs of Necturus are exposed on their ventral, medial and lateral surfaces, and are only incompletely covered on the dorsal by the fenestrated cartilage. In the origin of the columna ethmoidalis and its subsequent direction of growth, together with the development of the fenestrated roof, there is a similarity to Amblystoma; but the many striking contrasts between the capsules of these two Urodeles must establish very remote relationships between them, or are possibly to be interpreted by the neotenic character of this animal.

The lack of skeletal protection for the nasal organs, the absence of many parts of a typical urodelan capsule, as well as the very unspecialized nasal sac itself, suggests for Necturus that it is to be regarded as either ancestral, as a permanent larva or as indicating degeneracy of parts. To regard Necturus with its fenestrated capsule, which has no counterpart

throughout the entire urodelan order, as primitive, would be unjustified; but, the greatly retarded process of chondrification, the absence of cristae and cornua trabeculorum, together with the entire separation of the roof of the capsule from the other parts, may be explained in either of two ways; Necturus has either descended from some more specialized Urodele, or, as the retarded process of chondrification would suggest, it may represent a neotenic condition of some form, like Spelerpes.

AMPHIUMA MEANS

The first of the three capsules of Amphiuma studied, is that of a larva still within the egg, in which the chondrocranium is very incomplete, resembling in many ways the larva described by Kingsley (1892), and figured by Winslow (Fig. 18, 1898).

Each trabecula, from the crista forwards, inclines, at first gradually, and then somewhat more abrupt, toward the median line; the two uniting to form a small rectangular planum basale (*pb*, Fig. 29), which supports the olfactory lobes. Anterior to the planum, each trabecula continues forward a short distance, and then expands into a triangular cornu, concave upon its dorsal surface to support the anterior part of the olfactory sac. The cornua are separated from each other by a deep and narrow internasal space, resembling that of Spelerpes, the Urodele, the larva of which most resembles the early Amphiuma.

The cristae trabeculorum (*cr t*) are well developed and extend forward to the base of the antorbital process (*pa*), which in Amphiuma is directed obliquely forward from the trabecula, rather than at right angles to it as in other Urodeles. The anterior margin of each crista trabeculae is continued forward as a cylindrical bar along the medial dorsal margin of the nasal sac. At the level of the anterior end of the antorbital process, the bar runs forward and outward and passes obliquely over the nasal organ, giving rise to a short process just dorsal to the nasal sac, and continuing outward and downward to the lateral surface of the sac where it turns directly forward and runs along the lateral surface of the sac nearly to the level of the planum basale. Hay (1890) speaks of this bar as the rudimentary nasal capsule, while Winslow (1898) describes it as projecting forward, outward and downward, but without the small dorsal processes present in my stage, and which help to explain the later modifications of the capsule. In its origin from the trabecular crest, this bar, which probably contains elements of both ethmoidal column and tectal cartilage, recalls the process in Spelerpes, extending forward from the anterior margin of the crest, which was interpreted as the posterior end of a developing columna ethmoidalis.

Olfactory foramina do not exist, but each olfactory nerve passes over the trabecula just in front of the crista trabeculae, where the nasal organ and the olfactory lobe are very close together.

In an older larva, a more complete nasal capsule (Fig. 30) has been formed, which resembles in but few respects those of other Urodeles. It is somewhat ovoid in outline, its greatest width being about one-fifth its length. From the anterior end of the crista, each trabecula, relatively more slender than before, inclines medially and passing along the lower margin of the olfactory lobe, unites with its fellow at about the level of the middle of the capsule, to form the planum basale (*pb*). This plate is considerably larger than before, and together with the cornu of either side, forms a plate roughly hexagonal in outline. Its posterior margin is straight, while lateral to the line of the trabecula, its caudal margin is directed antero-laterally to a point corresponding to the lateral angle of the cornu of the early stage, where it fuses with another cartilage bar yet to be described. Each lateral-cephalic margin is also curved and is produced in front, in a line with the trabecula, into a process directed forward from the planum, the anterior extension of the trabecula. These cornual tips are separated by an internasal space somewhat wider although much shorter than before.

The planum verticale (*pv*) arises from the anterior half of the basale, just back of the internasal space, as a narrow band of cartilage, which separates the nasal organs in this region (Fig. 69, *pv*). Dorsally the planum verticale divides into two bars, the alary processes, which are inclined to each other at about an angle of 60 degrees. Each alary process is continuous with the columna ethmoidalis, and partially covers the antero-median surface of the olfactory sac.

The columna ethmoidalis is now complete, extending forward from the crista to, and slightly beyond, the alary process. Apparently this corresponds to the bar arising from the superior margin of the crista of the earlier stage, as far as and including the small process dorsal to the nasal sac described above. The more lateral portion of the earlier bar is evidently the lamina externa of this stage, which now extends forwards along the lateral surface of the nasal organ. At about the level of the planum verticale, the lamina externa (*le*) sends a process downwards, which unites with the lateral angle of the cornu. The lamina externa continues beyond this junction as a broader plate, ending in an oblique circumnarial cartilage ring surrounding the narial aperture.

The antorbital process is much as before, being inclined at an angle of about 30 degrees from the trabecula, rather than at right angles to it as in most other Urodeles.

Many of the characters of the nasal capsule of the adult Amphiuma, as described by Wilder (1892), appear in a larva 82 mm. long. The nasal capsule (Fig. 31) has doubled in size, although the proportions are unchanged; additional chondrification having occurred in the anterior parts. The crista trabeculae, antorbital process, trabecula, planum basale, and

columna ethmoidalis are much as in the younger stage, and need no further description. The dorsal surface of the capsule, however, has been changed by the continuation forward of the ethmoidal column to a junction with the circumnarial cartilage and a lateral extension of the cartilage from the column to the lamina externa; so that the whole anterior end of the capsule is roofed in as far back as the level of the verticale, this roof being perforated behind and near its median line for the passage of the nasalis internus of the profundus. The lamina externa, behind its connection with the cornu is wider than before, and close to the lower margin near its anterior end is a smaller foramen for the nasalis externus of the profundus, where it passes to the external nasal glands.

The chondrification of the anterior parts of the capsule has outlined a large gap upon the dorsal surface, bounded by the columna ethmoidalis, lamina externa and anterior tectale, resembling in shape the large dorsal gap in Amblystoma. The floor of the capsule is represented by the cornu trabeculae and the antorbital process; the latter has not united to any more anterior capsular part, so that a foramen orbito-nasalis does not exist, nor does Wilder describe one in the adult.

The nasal capsule of Amphiuma differs considerably from that of any urodele thus far described. The large vacuities in the dorsal, lateral and ventral surfaces and the consequent lack of skeletal protection of the nasal epithelium is much in contrast to either Salamandra or Amblystoma and may represent either a reduction in parts or a permanent larval condition. So far as I know, a circumnarial ring does not exist in any other Urodele, the anterior part of the capsule being vaulted in all others, with the exception of the Caecilians and Necturus. The fusion of the planum basale with the cornua trabeculorum to form the hexagonal plate, is not common for other capsules, where in the older stages these parts are considerably removed from each other.

The narrow planum verticale develops dorsally from the median line of the planum basale, somewhat as in Cryptobranchus, and then unites laterally to the ethmoidal column which, as in Spelerpes, probably developed anteriorly from the cephalic margin of the trabecular crest. In no other capsule, thus far described, with the exception of Necturus, is there a complete absence of the lamina medialis. Anterior to the verticale the nasal organs are separated by membrane only, a wide gap extending from the medial margin of the cornu to the anterior tectale.

Amphiuma appears to be far removed from other Urodeles. It cannot be regarded as ancestral, as it is difficult to homologize the capsule of this animal, even in the early larval stages, with that of other genera; but it probably is reduced from more typical conditions more closely related to either Spelerpes or Cryptobranchus. In the origin of the verticale and in the form of the cornu which unites to the anterior extension of the externa,

Amphiuma resembles Cryptobranchus; and furthermore, the expansion of the ethmoidal column, at its middle to form the lateral parts of the capsule is alike in both. On the other hand, Amphiuma resembles Spelerpes in the size of the planum basale and the inter-nasal space, as well as in the posterior development of the ethmoidal column, evidence being lacking on this point in Cryptobranchus.

THE NASAL CAPSULE OF THE GYMNOPHIONA

EPICRIUM GLUTINOSUM

Considerable diversity of opinion has existed in the past in regard to the systematic position of the Caecilians. Cope (1889) classed them as a family of the Urodeles, related to them through Amphiuma; while the cousins Sarasin (1890), following Cope, also regarded them as Urodeles, considering Amphiuma a neotenic Caecilian. Kingsley (1902) reviewed the evidence as to the position of the group, showing that many points supposed to indicate relationships, were based upon erroneous statements or misconceptions and that the Gymnophiona are to be regarded as a distinct group, without any close relations to any other existing Amphibia.

To determine to what extent, if any, the nasal capsules of this group would shed light upon their relationships to the Urodeles, two larvae of Epicrium glutinosum were studied, in which chondrification was well advanced and the nasal capsules completely formed.

Peter (1898) has described the chondrocranium of a young Caecilian; and Winslow (1898) a stage in which the embryo is still spirally coiled within the egg, considerably younger than my earlier material. In contrast to all other Amphibia, the trabeculae of each side are double (Fig. 32), consisting of a dorsal and ventral bar in the position of trabecular crest and trabecula, the dorsal doubtless being the homologue of what Sewertzoff (1897) has called the alisphenoid cartilage of the Elasmobranchs. On either side of the eye, the dorsal and ventral trabeculae are united by a postorbital and preorbital band, the optic nerve passing through the large gap between them. Anterior to the preorbital band, the lower or true trabecula inclines toward the median line, and is united with its mate by a slightly convex planum basale (*pb*), which lacks the trabecular thickenings of the plana of Urodeles. The posterior and lateral margins of the planum are straight, the latter more anteriorly curving outward where it passes into the posterior margin of the cornu trabeculae, which forms the floor of the capsule; while anterior to the cornu the planum narrows considerably and is continuous in front into a pair of small processes, the tips of the trabeculae, separated from each other by a wide internasal space.

The planum verticale (*pv*) is a narrow plate of cartilage, arising from the anterior half of the median line of the basale and extending dorsally

to the upper margin of the nasal organs, completely separating them in this region from each other. The dorsal part of the verticale extends backward a short distance over the planum basale; while anteriorly it extends forward over the internasal space where it divides into three parts, a short median rostrum continuous with the verticale, and a pair of alary processes which extend ventrally and laterally, terminating near the tips of the trabeculae. In a later stage these alary processes develop anteriorly and laterally to form the vault of the capsule.

Anterior to the preorbital band, a wide band of cartilage, the lamina externa, forms the side wall of the capsule. It is pierced by two foramina, the smaller more posterior one for a small branch of the fifth nerve, while the profundus passes through the larger, more anterior one. Winslow (1898), in his early stage, describes a small antorbital process which extends outwards and forwards from the anterior margin of the preorbital band, much as in the Urodeles. In this stage, the anterior part of this process has united to the lateral parts of the capsule, enclosing the foramen above described, which must be the orbito-nasalis of Urodeles; so that it would seem that the lamina externa is formed of elements of an ethmoidal column and an antorbital process, although complete evidence as to the former is lacking.

Anterior to the foramen orbito-nasalis, the lamina externa widens slightly, its dorsal margin extending more medially, reaches to the level of the upper surface of the verticale, where a short process extends forward, separated from the remaining externa by a deep notch through which the superficialis passes to the nasal organ. Ventral to this notch and in the same horizontal line with the foramen orbito-nasalis, is another foramen through which a branch of the profundus nerve passes from the capsule.

Beyond this latter foramen, the lamina externa, more narrow than before, extends forward a short distance, ending in a blunt process in line with the anterior margin of the planum basale; while ventral to the foramen it is united to the cornu trabeculae, which supports the anterior end of the nasal sac, forming the only floor of the capsule, and enclosing the large ventral choanal gap.

Winslow has described a small cartilage bar, lying near the trabecula, just beneath the preorbital band, which is unassociated with any other part of the capsule. This he calls a palatine cartilage. In my material, this small bar is directly in line with the anterior part of the pterygoid process from which it is but slightly removed; and it would seem as though it was a part of the pterygoid which may have chondrified independently, or have separated from the more basal part of this process. Peter (p. 582, 1898) in his description of the pterygoid of Ichthyophis says: "Dagen findet sich in seiner Verlängerung parallel der unteren Trabekelspange ein

Knorpelstab, der sich bis in die Mitte des Opticusfensters erstreckt und seinerseits wieder in zwei Theile gespalten sein kann. Eine dichte Zellanhäufung verbindet die einzelnen Stücke mit einander und mit dem Fortsatze des Quadratum, so dass die betreffenden Elemente wohl als eines Ursprungs aufgefasst werden können." The term palatal cartilage is a misnomer at least, for it is evident that the palatine bone, which is membrane in origin, could hardly be derived from this cartilage

The capsule of the older larva, 90 mm. long, (Fig. 33) differs considerably from that just described; the greatest change taking place in the more anterior parts. The ossification of many of the covering bones, and the resorption of certain cartilage structures, as well as the chondrification of others, has resulted in a capsule very different from that of any other Amphibian.

The preorbital and postorbital bands are much as before and need no further description, with the exception of the statement that they are more oblique, from medial and dorsal to lateral and ventral, than before. Through resorption, all connection between the preorbital band and the planum basale has been lost, so that a short caudal process from the planum on each side of the median line is a remnant of a trabecula, all intermediate parts having become ossified. The planum basale is shorter than before and the solum nasale or cornu trabeculae is now more posterior and in line with the caudal margin of the basale, which it unites to the lamina externa as in the early stage. The antero-lateral margin of the planum is more semicircularly excavate than before, and the tips of the trabeculae, extending beyond the basale are more slender, the internasal space between them being wider and deeper.

The planum verticale (*pv*), arising from the median line of the basale is wider than before, although not relatively as high. It is continued posteriorly into an elongate cylindrical process which extends backward to the level of the posterior margin of the basale, the dorsal root of the olfactory nerve lying lateral to it; while anteriorly it extends forward into a similar process reaching nearly to the tip of the snout. The alary processes, flanking the median rostrum of the verticale, which were just beginning to chondrify in the earlier stage, have now grown forwards and outwards covering the more anterior parts of the nasal sac and uniting with two lateral processes yet to be described, each forms a partial cupola, incomplete ventrally which protects the anterior ends of the olfactory sac. There is a small foramen near the lower margin of this cupola, through which a branch of the profundus nerve leaves the capsule.

The lateral wall of the capsule of this older stage is considerably different from that described above. The orbito-nasal foramen, the medial process of the lamina externa and their nerve relations are as before; but ventral to the foramen for the externus branch of the profundus, the

lamina externa bears a short posterior process from its ventral margin, a remnant of resorption now going on, so that the choanal gap in this stage is incomplete.

Just in front of the connection of the lower margin of the lamina externa to the cornu trabeculae, the lamina continues forward as two cartilage bars, the upper more cylindrical, the lower somewhat flattened, between which the organ of Jacobson is included. By the fusion of these parallel rods with the alary process above described, an elongate naris is formed which extends over one-half the entire length of the capsule; and at the same time these cartilages all unite to form the tip of the capsule, a flattened plate which covers the end of the nasal sac (Figs. 67, 68).

The nasal capsule of Epicrium is considerably different from that of any other Amphibian and can hardly be said to be Urodelan. In a very few points, resemblances can be drawn between the Caecilian and Urodelan structures; but these are so few, and the modification of the parts in the Caecilian is so great, that few close relationships can be established. The independence of alisphenoid cartilage and trabecula in Epicrium, find no parallel among the Urodela where these parts are continuous and form the wall of the cavum cranii; while in no other capsule do we find the deep and narrow external naris, as is present in my older stage.

The floor of the capsule is formed by a cartilage called by Peter (1898) the solum nasale, which can be none other than a modified cornu trabeculae which has developed laterally and has united to the lamina externa, just anterior to its fusion with the antorbital process. So that in this relation of cornu trabeculae, lamina externa and processus antorbitalis, there is a condition quite similar to the other capsules, such as Triton and Amblystoma, although superficial resemblances are lost. That the solum nasale was a cornu could not be derived from a study of the later stage where the greater development has taken place anteriorly, placing the solum in line with the planum basale; but the resemblance between the cornu trabeculae of my two weeks Cryptobranchus larva and this structure in my younger Epicrium seems to indicate the identity of these parts.

Superficially, the capsule of Epicrium resembles that of Amphiuma more than any other Urodele. In both the sensory parts are but poorly protected, wide gaps occurring in all sides of the skeleton. The presence of a six-sided planum basale, with its anterior prolongations, the planum verticale with its antero-lateral alary processes are structural resemblances between these animals. On the other hand Epicrium lacks the circumnarial ring of Amphiuma, and in its place has developed a partial cupola, possibly in correlation with the burrowing habit of this Amphibian.

In the origin of the planum verticale from the basale, as well as in the similarity of their cornua, Epicrium recalls Cryptobranchus; and it does not violate probability to assume that the small process developed

from the medial margin of the lamina externa is a remnant of an ancestral ethmoidal column, which originally was united to the more medial parts of the capsule.

Although some homologies may be drawn between the capsules of Epicrium and the Urodeles, the divergence between the two is sufficient to warrant the separation of the Caecilians and the maintenance of the Gymnophiona, distinct from all other Amphibia. Although the greater resemblance among the Urodeles is to Amphiuma, yet it is not sufficient to warrant the position of either Cope or Sarasin in the relationship of these groups.

COMPARISON OF THE NASAL CAPSULES IN THE URODELA AND GYMNOPHIONA

The nasal capsules of several families of Urodeles afford a basis for the division of this order of Amphibia into four groups, founded upon similarity of larval structures and the method of chondrification. In some forms, where larval characters were not at hand, adult characters were employed in the classification; in others the early process of development was the only criterion available. Of these groups, Spelerpes, Plethodon and Amblystoma form one; Salamandra, Triton and Diemictylus another; Amphiuma, although remote from Cryptobranchus in the later stages, is included with it in the third; while Necturus remains alone in the fourth group.

To recognize in the nasal capsules of the Urodela a complete phylogenetic development or gradual transition from one animal to another is impossible, for many gaps exist, concerning which evidences of structural relationships are wanting. On the other hand many resemblances in the development of certain structures in the nasal capsule may throw some light upon the inter-relationships of this Amphibian order.

Of the Urodeles included in this study, it would seem as if the capsule of the American species of Cryptobranchus possesses characters most ancestral and which show relationships to both Urodela and Anura. Regarding Cryptobranchus, then, as more primitive, Spelerpes, Plethodon and Amblystoma appear in an ascending series from the primitive condition; while Salamandra, Triton and Diemictylus are separated from them, but possibly related to them through some form like Spelerpes. Necturus may be regarded as a neotenic condition of Spelerpes, while Amphiuma is possibly reduced from the more primitive Cryptobranchus.

The two weeks larva of Cryptobranchus has a well-developed trabecular crest which is not present in corresponding stages of Spelerpes or Amblystoma; in the latter of which the development of the crest is apparently correlated with the chondrification of the ethmoidal column. Thus it would appear that in Cryptobranchus the dorsal crest is developed before the column, while in Amblystoma the reverse is true. In this respect, Spelerpes is intermediate between Cryptobranchus and Amblystoma, although more like the former; for in the only available stage of the older larva of Spelerpes, the crista is well developed, while the columna ethmoidalis is but partly chondrified. My material does not show the origin

of the ethmoidal column in Cryptobranchus, for in the five weeks larva it already unites the medial margin of the cornu to the crista; but judging from its relation to the capsule, and in its complete separation from its mate, these structures resemble those of Spelerpes in which the anterior part of the columna arises from the medial margin of the cornu and grows posteriorly along the nasal sac. Further, the anterior prolongation of the dorsal crista in Spelerpes, interpreted as the posterior part of a developing column, may also exist in Cryptobranchus, although conclusive evidence on this point is lacking.

In the 25 mm. Salamandra larva, the anterior end of the column is connected to the cornu trabeculae much as in Cryptobranchus; and yet the expansion from its posterior end, forming a small tectale prior to any connection with the crista, suggests an independence of the ethmoidal column, like that of Amblystoma. Although the dorsal crests of Salamandra develop along with the columna ethmoidalis, the two do not unite until a later stage, thus the posterior part of a developing column is lost in all Urodeles above Spelerpes. In Amblystoma, on the other hand, the ethmoidal column and the cornu trabeculae are chondrified independently of each other. In a 13 mm. larva, I have described a few cartilage cells above the medial margin of the cornu of the left trabecula only. This is the first appearance of an ethmoidal column which subsequently grows posteriorly along the median dorsal margin of the nasal sac. The fact that I observed these cells as chondrifying, at first, upon one side only, has no especial significance; but in the independent chondrification and the complete development of the ethmoidal column from in front backwards, prior to any association with the trabecula, Amblystoma differs from any other Urodele, except Necturus in which the independently chondrified ethmoidal column never unites to other parts of the capsule. Thus in the 20 mm. stage of Amblystoma, completely developed columnae ethmoidales parallel the trabeculae from their anterior tips to the choana; but do not unite to any crista, which here is greatly retarded in its appearance, not developing until the 25 mm. stage is reached.

The ethmoidal column in Amphiuma is more like that of Cryptobranchus and Spelerpes in the development of the posterior parts; there being no evidence of an anterior part of a column in the youngest larva studied. Somewhat as in Spelerpes, the anterior portion of the crista continues forward into a cylindrical bar along the medial margin of the nasal sac, and from its relation to other parts, as well as its position, it must be regarded as a columna ethmoidalis. As in Cryptobranchus, it gives off laterally a small process which may be homologized with the tectale, which then turns anteriorly, forming the lateral wall of the capsule, the lamina externa.

In all Urodeles studied, the planum basale is formed by a fusion of the trabeculae in the middle line of the skull; and in some forms, this plate,

which usually supports the anterior end of the telencephalon, is the only connection between the two capsules. In Cryptobranchus, Amphiuma, and Necturus, the planum basale of the larval stages is slightly convex, due to the origin of the verticale from its median line; while on the other hand the planum basale of Salamandra and Amblystoma are broadly concave, being in no way associated with the development of the verticale. The size of the basale is variable in the different groups; being very small in Cryptobranchus, Spelerpes and the larval Amphiuma, it increases in Plethodon and Salamandra, and reaches its greatest development in the larvae of Amblystoma where the fused basale and verticale form a thick anterior wall to the cavum cranii. Individuals approaching the end of metamorphosis show a reduction in the size of the planum basale, and in the adult stage it is greatly reduced, correlated with the development of other parts of the capsule and the increase in size of the sensory parts. In both larvae and adults of Triton and Diemictylus the planum basale is very small, and in the latter, is the only connection between the two capsules.

The planum verticale arises in different ways throughout the order. In Cryptobranchus, it arises from the median line of the basale as a small ridge, and later, uniting to the median margins of the ethmoidal columns, it forms a complete wall separating the internasal space from the cavity of the forebrain. The same is true in Amphiuma, although evidence is lacking as to the origin of the verticale, yet the later stages would suggest its development from the planum basale as in Cryptobranchus. The early larvae of Necturus have a small median ridge on the basale, probably a vestigial verticale; but it never develops and is less prominent in the later stage, a further evidence of the neotenic condition of this genus.

In the remaining groups, the verticale does not arise from the basal plate, but is developed by medial growths from the columnae ethmoidales which subsequently unite to the basale, so that the results are identical. In my material of Spelerpes, evidence of the formation of the verticale is lacking; but judging from the relation of the early columna to the cornu, and by the flat dorsal surface of the basale, it would appear that here, as in Amblystoma, the verticale arises from the medial growths of the ethmoidal columns. In a 25 mm. Salamandra larva, there is no evidence of a median verticale plate. The cornua and columnae are united just anterior to the planum basale, but internasal space and cavum cranii are continuous with each other. In the later stage, medial growths from the anterior parts of the columnae unite just above the anterior margin of the basale, and form a pons ethmoidalis, separated from the ventral plate by a circular gap, the fenestra ethmoidalis. This gap is only temporary in Salamandra, for by the more ventral chondrification of the pons, a complete verticale is formed and the internasal space and cavum cranii are completely cut off from each

other. In Amblystoma, this process is changed slightly, due to the independence of the ethmoidal columns from the cornua. In the 25 mm. larva, by medial growths of the columnae a pons has formed, so that in this stage the capsule is divided into dorsal and ventral halves, the only connection being the crista. By further chondrification of the region between the pons and the planum basale, a verticale is formed, the process continuing posteriorly, developing the solid thick cartilage of the 45 mm. larva.

A planum verticale does not chondrify in Triton and Diemictylus, so that internasal space and cavity of the forebrain are separated by membranous structures only. The pons ethmoidalis develops in Triton, uniting the dorsal medial margins of the capsules somewhat anterior to the planum basale, but it is completely lost in Diemictylus. Evidence is lacking as to the origin of the pons in Triton, but Born (1876) describes the process as a continuous growth of cartilage from the trabeculae, and not as independent parts; it would appear, then, that the pons has probably arisen by growths from the medial surfaces of the capsules, similar to that of Salamandra. In the absence of a pons, Diemictylus appears to be reduced from some form like Triton; the nasal capsule of these two being very similar in other details.

The antorbital process is present in all Urodeles, arising in all, except Cryptobranchus, from the ventral margin of the trabecula just back of the choana. It is directed laterally and anteriorly and in most Urodeles unites to the lamina externa, or to the cornu trabeculae, outlining the foramen orbito-nasalis, through which the nerves of the nasal region enter the capsule. In Necturus and Amphiuma, on the other hand, this process never unites to the more anterior parts of the capsule, so that a foramen is never formed, nor is there any posterior wall to the capsule as in those Urodeles where the antorbital unites to the tectale, as in Plethodon and Amblystoma.

Gaupp (1893) held that the antorbital process of Urodeles is homologous with the pterygo-quadrate arch of the Anura; and the terms palatine cartilage or ethmo-palatine have been indiscriminately used when referring to this structure. If we regard Cryptobranchus as ancestral, or at least more primitive, a conclusion I believe both the nasal capsule and the olfactory organs justify, then the relations and the development of the antorbital process in this animal may throw some light upon the homology of these structures. In the two weeks larva, in which the trabecular crests are already well-developed, there is no evidence of an antorbital process; but slightly posterior to its probable position, procartilage cells lie near the lateral ventral margin of the trabecula, which continue posteriorly into the pterygoid process of the quadrate. In the later stage, these cells have chondrified and, uniting to the pterygoid, have reached

forward, and, bending at right angles the bar has joined to the ventral margin of the trabecula in the region where the antorbital process occurs in all Urodeles. In the five weeks larva, there is no extension forward of this bar beyond its connection with the trabecula; but in the older larvae, a small process extends forward toward the capsule, an apparent continuation of the pterygoid; so that an antorbital process is formed which resembles in detail those of most other Urodeles. Because of the lack of older stages, I have no evidence as to the connection of the antorbital to the capsule, nor can I say just when the resorptive processes take place which establish the adult condition of the complete separation of the pterygoid from the capsular region.

Regarding Cryptobranchus as primitive, then it would appear that the Urodelan antorbital process is in reality composed of the anterior end of a pterygoid plus an anterior extension which secondarily becomes associated with the nasal region. In the Anura, both larva and adult, the pterygoid unites with the anterior part of the trabecula, as in the larval Cryptobranchus, suggesting here a common ancestry; and this relationship tends to support the original conclusion of Gaupp that the antorbital process of Urodeles, at least in its basal part, and the "palatine cartilage" of the Anura are homologous structures. The anterior part of the antorbital, however, is something else and may not be a part of the original pterygoquadrate arch; accordingly it would seem that in those Urodeles in which the pterygoidal condition is lost, that the entire structure had best retain the name antorbital process.

Winslow (1898) has described, in his second stage of Ichthyophis, an isolated cartilage in front of the anterior end of the pterygoid, which he calls the "palatine cartilage"; and interprets it as being a part of an original "palato-pterygoid-quadrate" arch. This cartilage can hardly be called a palatine, and the triple term applied to the pterygo- quadrate is a misnomer for the palatine bone is not cartilaginous in origin. It would appear, however, as though this small cartilage is a part of the pterygoid which at one time was connected to the antorbital process, and to the more proximal pterygoid. In his earlier stage, Winslow describes a small antorbital process which arises much as in the Urodeles from the trabecula. In my material, this process has united to the more anterior parts of the capsule outlining the foramen orbito-nasalis; and from its relation to the isolated part of the pterygoid we are safe in assuming that these parts were at one time in continuity, and in that sense the Caecilians are related to the common ancestor, from which Cryptobranchus on the one hand, and the Anura on the other, have arisen.

In the Siberian genus, Ranodon, Wiedersheim (1877, Fig. 69) has figured the relation of the antorbital process to the pterygoid much as it occurs in Cryptobranchus; which fact suggests that these genera may be

related, both having retained these ancestral characters. An older larva of Spelerpes, also figured by Wiedersheim (Fig. 108), has a caudal extension of the antorbital process, which he calls the maxillary cartilage, whose relation to the pterygoid suggests an earlier relation between the two.

In several of the Urodeles, as shown by figures of Parker (1876), and Wiedersheim (1877), a strong pterygoid reaches well forward from the quadrate, absent in some of my larvae but present in the adult. In the earlier larva of Amphiuma, a pterygoid process has not developed; but in the later stage it has chondrified well forward, nearly to the base of the antorbital. In all Urodeles, both processus antorbitalis and pterygoid are developed, but the proximity of the two varies greatly throughout the order, and I would hesitate to base any statement of relationships upon the relative extent of development of these structures; but no where except in Cryptobranchus and Ranodon is there any connection between them.

The openness of the nasal capsule of Amphiuma, together with the somewhat specialized anterior part, renders it difficult of homology with the more typical Urodele, and suggests that it is far removed from any other Amphibian. However, in the early method of chondrification, and in the development of some of the parts, Amphiuma appears to be more closely allied to Cryptobranchus. In both, the cristae trabeculorum are formed early, as well as the planum verticale, the latter arising from the median line of the basale and later becoming associated with the columna ethmoidalis. Further relationship is evidenced in the origin of the tectale as a lateral growth from the columna, giving rise in Amphiuma to the elongate lamina externa, along the lateral surface of the nasal sac. Meagre as these relationships may seem, Amphiuma appears to be nearer Cryptobranchus than any other Urodele, the anterior parts of its capsule having become secondarily acquired.

Although Salamandra resembles Amblystoma in some ways, the many differences between their capsules, such as the size of the planum verticale, the persistence of the foramen ethmoidalis in the former, and the origin of the ethmoidal columns, justifies their separation. In the persistence of the caudal process of the planum basale in the 25 mm. Salamandra, there is a resemblance to Cryptobranchus; but in the origin of the columnae ethmoidales from the medial margins of the cornua, Salamandra is more like Spelerpes.

Triton and Diemictylus are far removed from the group just described, but are probably related to it through Salamandra. The complete development of a lamina medialis, with the deep internasal space, and the anterior position of the olfactory sac in respect to the forebrain, as well as the persistence throughout life of the fenestra ethmoidalis, are characters common to both Triton and Diemictylus. The complete loss of a pons ethmoidalis in Diemictylus converts the fenestra into a gap, only a mem-

branous partition separating the internasal space from the cavum cranii. It would follow then, that Diemictylus is probably reduced from some form like Triton, and both genera are related to Salamandra which has developed along a line parallel to Amblystoma; and it is through some Spelerpes-like larva, as far as the nasal capsules are concerned, that Salamandra, Triton and Diemictylus are related to the group including Plethodon and Amblystoma.

Necturus and Proteus have often been regarded as primitive and Cope (1889) included them in a group, Proteida, apart from the Urodeles, although ancestral to them. I have not examined Proteus, but upon the basis of the nasal capsule of Necturus, which cannot be regarded as ancestral, Cope's position can not be affirmed. Pinkus (1894) called attention to the similarity of the nasal capsules of Necturus and Protopterus, a similarity based wholly upon the fenestration of the capsules, and not upon structural resemblances. The parts of the capsule of Necturus may be homologized with those of other Urodeles, but many differences have arisen in the appearance of these parts, so that relationships are very remote. Many parts of the capsule chondrify independently, later uniting to each other; the ethmoidal column, however, never unites to the other parts of the capsule, but by lateral growths produces the fenestrated roof over the nasal sac. Necturus is greatly retarded in the development of its nasal structures. In a 25 mm. larva only trabeculae are present, there being no evidence of cornua or planum basale or columnae, as in corresponding ages of Amblystoma and Salamandra. The earlier larvae of Spelerpes, Desmognathus, and Necturus seem to resemble each other very closely in their cylindrical trabeculae, slight cornual expansions and absence of trabecular crests. In the later stages, however, further resemblance is lost, for Spelerpes has gained true Urodelan characters while Necturus still possesses larval relationships; a fact, which, together with the retarded process of chondrification, suggests for Necturus that it may be a persistent larva, as has often been suggested.

As stated above, Cope placed Proteus with Necturus in the Proteida, regarding them as primitive Amphibia, and related to the Stegocephala by the presence of an intercalary bone. Kingsbury (1905) rejects Cope's thesis, affirming the absence of an os intercalare in Necturus, and suggested that Cope had probably regarded the posterior process of the opisthotic as an intercalary; furthermore he regards the intercalary of the Stegocephala as a membrane bone.

Norris (1911) working on the cranial nerves of Necturus, concludes that it cannot be regarded as primitive. The distribution of the cranial nerves agrees in detail with that of the higher Urodeles, a condition which would not be expected in a primitive form. Kingsbury, like others, has regarded Necturus as a neotenic larva, and would place it near Spelerpes.

His conclusion is based largely upon the absence of certain cranial bones, such as the nasals, prefrontals and maxillaries, which are present in other Urodeles. Rudimentary nasal capsules exist in the larvae of both Spelerpes and Necturus, and in the former a completely developed capsule is not present until a relatively late period, correlated with its retarded metamorphosis, the individual often not transforming until two or three years after hatching. On the basis of the nasal capsule, I am inclined to regard Necturus as a permanent larva, possibly related to the other Urodeles through a Spelerpes-like ancestor. The retention of the larval characters of the trabeculae and of the planum basale can certainly not be regarded as ancestral, nor can degeneration alone explain the present structure of the capsule of Necturus.

The phylogenetic position of the Gymnophiona has occasioned much diversity of opinion. Huxley (1875) stated that there was not the slightest indication of any approximation to either the Anura or the Urodeles. On the other hand, Cope (1889) even placed the family Caecilidae among the Urodeles, and regarded them as degenerate and related to the main line through Amphiuma; while the Sarasin cousins (1890) took the position that Amphiuma was a neotenic condition of the Caecilian. Kingsley (1902) discussed the views of both Cope and the Sarasins and established the conclusion, now generally accepted, that the Gymnophiona are to be regarded as distinct from either Urodela or Anura and placed in a separate order.

The nasal capsule of Epicrium presents little of classificatory value, except that it presents only distant resemblances to the characteristic Urodelan capsule. In the presence of dorsal and ventral trabeculae, Epicrium differs from all other Urodeles where the alisphenoid and trabecula are continuous and form the lateral wall of the cavum cranii. In the earlier stage, which Winslow studied, the ventral trabeculae unite to form the planum basale, but there is no extension forward of the trabeculae into cornua as in Urodeles; although in my earlier stage, which is considerably later than that of Winslow, small processes occur at the anterior margin of the basale, the probable tips of the trabeculae. The solum nasale, however, or floor of the capsule which unites the lamina externa to the planum basale, is a modified cornu, which in the older stage especially, is greatly removed from the position of the cornu trabeculae in Urodeles. The antorbital process, a lateral growth from the trabecula in the early stage of Winslow, later unites to the other parts of the capsule, as in Urodeles, bounding the orbito-nasal foramen. That the antorbital was at one time related to the parts of the pterygoid just posterior to it, is suggested by a sharp protuberance on its ventral margin toward the small independent part of the pterygoid; so that it would appear as if the processus antorbitalis and pterygoid cartilage of Epicrium were at one time united as in

Cryptobranchus, but the now intimate association of the former with the nasal capsule indicates that the Caecilian probably is far removed from ancestral conditions.

Epicrium is more like Amphiuma, of all Urodeles, although differing greatly from it. The greater similarity lies in the origin of the planum verticale from the median line of the basale and in the subsequent development of the alary processes which, in the later stages of both, partially cover the dorsal surface of the nasal sac. Further similarity lies in the modification of the cornu trabeculae which in both, forms the floor of the capsule, uniting the planum basale to the lower margin of the lamina externa, and partially supporting the nasal organ.

On the other hand, the parallel rods of cartilage which in Epicrium form the lateral wall of the capsule anterior to the solum nasale, uniting anteriorly with the alary process to form a partial vault, do not exist in Amphiuma, where the united elements of cornu and lamina externa expand into an oblique circumnarial ring. Further, the antorbital process of Amphiuma never unites to the capsule as in Epicrium, nor at any stage does a complete columna ethmoidalis exist in the latter form, so that there are many contrasts between the capsules of the two. Thus upon the evidence submitted by the nasal capsules, the position of Cope or Sarasin can not be supported, all conditions pointing to the complete separation of the Gymnophiona from the Anura or the Urodela.

THE NASAL CAPSULES OF THE ANURA

PIPA AMERICANA

The Surinam toad, a representative of the aglossate Anura, is unique among the Amphibia in its quiescent larval period, during which, the entire development takes place; so that the adult characters are formed before the animal takes up its free existence.

Parker (1876) has described the chondrocranium of a Pipa larva, considerably younger than my single stage, in which the complete fusion of the trabecular plates has obliterated the large hypophysial fenestra, so common to most amphibian skulls. In Parker's larva, the coalesced trabeculae form a broad, slightly emarginate internasal plate, which extends forward to the tip of the skull, where from each lateral margin a slender process bends posteriorly and, passing beneath the nasal organ, terminates in a rounded projection near the middle line of the capsule. Parker calls these processes the 'recurrent trabeculae', but it is easy to see that they are modified cornua, which in Pipa are more cylindrical than in most Urodeles, more like those in Cryptobranchus.

In my single stage, a Pipa larva two-thirds of an inch long, much of the cartilage of Parker's stage has been resorbed and the chondrocranium is more like that of other Amphibia. The broad intertrabecular floor is now reduced to a pair of trabeculae, which, with greatly reduced cristae, reach forward to the level of the eye, where they are united by a planum basale as in Urodeles (Figs. 34, 35, *pb*). This planum basale is broadly concave dorsally (Fig. 73, *pb*), and supports the olfactory lobes which lie above the posterior parts of the nasal organ; so that the olfactory nerve, which leaves the olfactory lobe from its ventral margin, passes through a large median foramen olfactorius (*fo*) in the basale, reaching the nasal sac at the choana. More anteriorly the planum basale narrows considerably, covering only the medial parts of the nasal sac and the nasal glands; at the same time expanding ventrally into a prominent keel, which separates the choanae of the two sides. Farther forward the planum basale is continuous with the planum verticale, which reaches forward to the tip of the skull, there to unite with other parts yet to be described thus completely separating the nasal organs of the two sides.

From each lateral angle of the planum basale, a small planum tectale (*pt*) passes obliquely outwards and forwards, covering the posterior part of Jacobson's organ where it empties into the nasal sac. At its lateral

posterior angle the tectale is continuous with the anterior portion of the pterygoid process, the two uniting to form a large triangular plate, Parker's ethmo-palatine cartilage, which continues forward into his pre-palatine spur; this process covering Jacobson's organ and part of the nasal sac. It is obvious that the terms ethmo-palatine and pre-palatal spur, used by Parker, are misleading for reasons stated before in this paper; and it would seem that the term planum tectale had best be used to designate this entire process. The extension forward of the pterygoid is the normal condition in the Anura, but among the Urodeles it is known to exist only in Cryptobranchus and Ranodon, this ancestral character having been lost in other Amphibia.

On the lower outer surface of the trabecula, at its junction with the capsular parts, is the foramen for the nasalis nerve, hence this is the orbitonasalis of the Urodeles. It follows from this identification, that the bar ventral to this is the greatly reduced antorbital while the roof of the foramen is as plainly tectale. The main part of the nerve courses forward through the cartilage, and the anterior end of the foramen lies on the ventral side of the tectale (Fig. 35). Another branch of this nerve emerges on the dorsal surface of the trabecula, turns medially and then ventrally and passes through another foramen to the medial side of the nasal sac parallel with the olfactorius. Just medial to this last foramen is the olfactory foramen for the I nerve which passes downward to reach the olfactory organ. From this it follows that the cartilage region anterior (and morphologically dorsal) to these nerves and their foramina must be the columna ethmoidalis.

At about its middle, the lower margin of the planum tectale gives rise to a short bar, at first extending ventrally and then medially and a little posteriorly, just above the anterior end of the organ of Jacobson. From near its base this bar gives rise to a cylindrical rod, which runs obliquely forward and inward to become continuous with the lower lateral surface of the planum verticale near its anterior end. In this course it passes, first, on the outer surface of the connection of the organ of Jacobson with the olfactory sac, then along the ventral lateral margin of the sac itself. The medial end of the ventral bar is connected with a second cylindrical cartilage, passing obliquely forward and inward to join the dorsal lateral side of the verticale at its tip, medial to the naris. Where the more ventral of these two cylindrical bars unites to the verticale, it expands into an alinasal cartilage, which supports the anterior part of the nasal organ, and is separated at its anterior end from the distal margin of the verticale by a crescentic groove, the external naris (Fig. 74).

The two cylindrical cartilages just described, have been known in the literature as the dorsal and ventral bars or processes, terms that convey nothing as to their homologies. From a study of Parker's early larva, it is

evident that the planum verticale is a reduced internasal plate, and that the so-called ventral process is a modified cornu. In the early stage, according to Parker, this cornu trabeculae is free from the tectale, ending near its median margin in a blunt process; but in the stage that I have studied the two are united, thus recalling the relation of these parts in the Urodeles. The dorsal process is evidently something additional in Pipa and cannot be compared to any Urodelan structure; although it exists in some form or other in all Anura, where it has been called the oblique cartilage because of its relation to the nasal organ. This cartilage may be a part of the original internasal plate of Parker's stage, the intermediate part between it and the verticale having been resorbed, leaving the elongate gap upon the dorsal surface of the capsule.

The capsule of Pipa is unlike any other Amphibian, differing markedly from any Urodele or Phaneroglossa, although similar in many ways to the other aglossal genus Dactylethra. The chondrocranium of Parker's younger larva is more complete and lacks the large gaps of the later stage, in which the resorptive processes have so greatly changed the appearance of the capsule. The planum tectale is evidently a growth from both the columna ethmoidalis and the trabecula, and has subsequently become united posteriorly to the pterygoid process, while anteriorly it has grown forward into the triangular process which has erroneously been called the ethmopalatine cartilage.

From the above identification of the ethmoidal column, it would appear that the planum verticale has developed by a fusion, in the middle line of the skull, of the trabeculae and the columnae ethmoidales; the ventral part of the verticale being trabecular in origin, the dorsal half derived from the united columnae ethmoidales. In this relationship, then, we have a condition very largely Amblystomal; for in the 34 mm. larva, the ethmoidal columns unite to the coalesced trabeculae to form the thick planum verticale so characteristic of Amblystoma, but which in Pipa is so greatly reduced in width.

BUFO AMERICANA

The nasal capsule of the Phaneroglossa is far more complex than that of the Aglossa, and the olfactory organs which lie entirely anterior to the forebrain are better protected by cartilage structures.

In a larva of *Bufo vulgaris*, one-third of an inch long (Parker, 1876), the trabeculae have fused to form an internasal plate, smaller than in Pipa, from which they diverge forward forming the cornua trabeculorum with an internasal space between them. So that this early stage of Bufo is similar to my 28 mm. *Rana viridescens*, yet to be described.

In my single stage of *Bufo americana*, whose body length is 9 mm., a complex nasal capsule has been chondrified; and resembles in many ways

the chondrocranium described by Gaupp (1893) of a 13 mm. *Rana fusca*. In this stage (Figs. 36, 37), a complete cavum cranii has been formed, bounded upon each side by the high alisphenoid cartilage, the internasal plate or planum basale forming the floor; while in front a perpendicular ethmoidal wall, pierced by a pair of olfactory foramina, separate the olfactory lobes from the nasal sac. Anterior to this ethmoidal wall, the planum basale (*pb*) forms the floor of the capsule; extending forward as a thick plate as far as the large naso-basales fenestrae, which open from the cavity of the capsule to the internasal space. The planum basale supports the medial parts of the nasal sac and its ventral diverticulum.

The planum tectale (*pt*) forms the roof of the capsule; reaching forward from the cavum cranii, somewhat more narrow and thinner than the basale, it covers the medial portions of the nasal sac to the external naris, in front of which it bends abruptly downward to form with the solum anterius, the anterior wall of the capsule. At its anterior end, the tectale expands laterally into a pair of alinasal cartilages, which curve outward and then upward, supporting the anterior end of the nasal sac and forming the ventral margin of the external naris; while from the base of these a pair of superior prenasal processes extend downward and somewhat medially into the internasal space (Fig. 82). Just medial to the external naris, the tectale is pierced by a small foramen on either side for the exit of the internus branch of the fifth nerve.

The planum verticale (*pv*) completely separates the nasal organs from each other. Arising from the median line of the perpendicular ethmoidal wall, it chondrifies anteriorly uniting the plana basale et tectale by their dorsal and ventral surfaces respectively. It extends forward to the tip of the skull, and its anterior margin separates the two large circular naso-basales fenestrae, which perforate the forward wall of the capsule (Fig. 80). These fenestrae surround the medial portion of the ventral nasal diverticulum together with the frontalis nerve, which passes to the intermaxillary gland in the internasal space.

In contrast to Pipa, a posterior wall is formed in the capsule of Bufo, by a lateral extension of the posterior part of the planum tectale, which curves outward and downward beyond the alisphenoid, uniting to the anterior prolongation of the pterygoid, which has already fused with the lower parts of the cranial wall. In the angle formed by the fusion of the pterygoid, tectale and alisphenoid, a small orbito-nasalis foramen conducts rami of the fifth nerve into the capsule; so that here, as in Pipa, there is a resemblance to the Urodeles, which furnishes a clue to the homologies of these parts (*fon*).

The united elements of lateral tectale and anterior pterygoid form a small rectangular cartilage which lies against the lateral surface of the nasal sac. This cartilage has been variously named the pars plana (Parker

1876) or planum terminale (Gaupp 1893); but from its relation to the tectale and the pterygoid, and from its position in respect to the nasal sac, the term lamina externa is best used here. Furthermore, it is apparently, at least in part, the homologue of the antorbital process of the Urodeles. Parker has also used the term prepalatine for this cartilage, which appeared to him to be in some way segmented from the more posterior parts; but I have no evidence that the lamina externa in Bufo is distinct from the other parts, for it appears to develop as a continuum, subsequently uniting to the more anterior parts of the capsule.

From the dorsal margin of the lamina externa, a narrow bar of cartilage passes upward, forward and medially over the lateral surface of the nasal sac to unite to the lateral margin of the planum tectale, slightly posterior to the external naris. This is clearly homologous with the dorsal process of Pipa, better known in both groups as the oblique cartilage (Fig. 81). The lacrimal duct, arising from the eye by two branches, passes forward over this oblique cartilage and down through a groove in the lamina externa to empty into a lateral diverticulum of the main nasal sac (Fig. 80).

Anterior to its connection with the oblique cartilage, the lamina externa continues forward into the lateral margin of the solum anterius, which forms the anterior wall of the cavum inferius, and is evidently developed from the cornu trabeculae, together with a dorsal extension of it. It is a thin plate of cartilage, bent upon itself, so that it includes in the angle the anterior part of the cavum inferius, which contains the more lateral parts of the ventral pouch of the nasal sac. More dorsally the solum anterius unites to the anterior margin of the planum tectale, its lateral margin expanding into the alinasal cartilage, already described. More posteriorly and within the capsule itself, is a short cylindrical bar of cartilage which extends from the lower margin of the alinasal cartilage to the anterior margin of the planum basale, thus separating the main nasal sac from the organ of Jacobson.

A small cylindrical inferior prenasal process, larger than the superior, extends forwards and slightly upwards into the intermaxillary glands. Below and behind, from the lateral angle of the solum anterius, a short process is directed posteriorly which rests beneath the diverticulum of the nasal sac, where it receives the lacrimal duct. This process may possibly be the tip of the cornu.

In contrast to Pipa, the capsule of Bufo much more adequately protects the olfactory organs; the gaps in its wall being smaller than in that genus. In Bufo the choanal fenestra is small and is distinctly bounded by cartilage, while in Pipa its boundaries are decidedly indefinite. Again Pipa has no circumscribed fenestra naso-basalis. Further differences between the capsules of the two genera are the greater depth of that of Bufo, correlated with a reduction in length, the result being an apparently more complicated condition of the anterior parts.

HYLA PICKERINGII

My work on Hyla has been restricted to a study of the adult, in which the development of membrane bones over the anterior end of the forebrain has been accompanied by a partial resorption of the posterior parts of the capsule, so that homologies are not always certain. Still Hyla in general has a somewhat close resemblance to its arciferan relative, Bufo.

Behind the planum verticale (*pv*), the planum basale (*pb*) has undergone resorbtion in the middle line, so that it is represented by a pair of narrow plates (Fig. 38). In front, however, the continuity of the two sides persists to the anterior end of the capsule, where the planum basale passes into the solum anterius. The perpendicular ethmoidal wall is lacking, as well as the posterior part of the planum tectale, so that the latter, posteriorly is reduced to an oblique bar on either side, the tectale being complete only in its anterior third, where it is expanded in front to twice its width. At the tip of the cranium, the tectale bends downward to pass into the vertical solum anterius.

All that remains of the planum verticale (*pv*) is a median septum, without a gap, uniting the anterior parts of plana basale et tectale. In front, where it joins the solum anterius, the tectale separates the two basal fenestrae, which are very much smaller than in Bufo. Dorsal and slightly lateral to these openings, is a small foramen for the exit of the nasalis internus nerve from the capsule.

The lamina externa (*le*), developed partly from the lateral part of the planum tectale, and partly from the anterior prolongation of the pterygoid process, forms the side wall of the capsule in the choanal region. Anterior to its connection with the tectale, this plate narrows considerably, and is interrupted by an oval gap, apparently a further evidence of resorbtion, as no sensory or nervous structures were found to pass through it. Just anterior to this opening the oblique cartilage (*oc*) passes upward and forward from the lamina externa over the nasal sac, to unite to the planum tectale at its widest part, its ventral side being expanded to form the posterior boundary of the naris (Fig. 77).

Just ventral to the origin of the oblique cartilage from the lamina externa, the lower margin of the latter expands outward into a small process which separates the cavum inferius from the more ventral cavum medium. More anteriorly, this part of the lamina externa unites with the lateral parts of the planum basale to form the solum anterius, which constitutes the anterior wall of both cavum inferius and c. medium, and the more medial parts of the capsule.

As in Bufo, the solum anterius is a thin plate of cartilage which curves upward and continues into the anterior margin of the planum tectale. Near its junction to the latter, a small alinasal cartilage extends laterally, forming the anterior boundary of the external naris; it is continuous med-

ially into a small superior prenasal process which extends ventrally and medially from the capsule. The inferior prenasal process is considerably longer than the superior; it arises from the planum basale just in front of the choanal gap and extends forwards and downwards into the internasal space (Fig. 78). Forming the floor of the c. medium, and extending backward beneath and slightly lateral to the lamina externa is a conical process considerably larger than that in Bufo; the possible remnant of the original cornu trabeculae.

Two small foramina pierce the solum anterius; the smaller and more dorsal conducts the nasalis internus from the capsule, while the larger more medial one is the fenestra naso-basalis, considerably smaller than that described for Bufo.

RANA VIRIDESCENS

The nasal capsules of the Arcifera and the Firmisternia are essentially alike, and, although I lack a series of stages showing the chondrification of the nasal capsule in Rana, the work of Gaupp (1893) has made it possible to compare the growth of the nasal capsule of the frog in connection with my own two stages.

In a larva 28 mm. long (entire length), in which the characteristic Anuran chondrocranium is beginning to develop, the nasal capsule (Fig. 40) consists of an elongate planum basale (*pb*), with the anterior extension of the trabeculae to the labial cartilages. The muscularis process of the quadrate (*mpq*) has fused with the lateral wall of the planum basale, and just above the junction of the two a dorsal process has arisen from the basale, which is to become the side wall of the capsule (Fig. 83). Gaupp (1893) has referred to this cartilage as the "Ethmoidal-pfeiler," but it differs from the ethmoidal column of Amblystoma in which chondrification of this bar is independent of the planum basale.

Medial processes from the dorsal margin of each columna ethmoidalis fuse in the middle line and form a pons (*pe*), recalling this same structure in Amblystoma and in Salamandra (Fig. 84). In all three genera the cavum cranii and the nasal cavity are continuous during a part of the larval development by means of the fenestra ethmoidalis (*fen eth*) ventral to the pons. Unlike Triton and Diemictylus however, chondrification from the pons to the planum basale soon develops the ethmoidal wall which separates these cavities.

Upon a level with the pons ethmoidalis, and arising from the dorsal part of the ethmoidal column, a small process extends laterally toward the muscularis process of the quadrate. A small opening, which must be regarded as the foramen orbito-nasalis for the nasalis internus nerve, pierces this process near its base; and from this identification, it follows that this process must contain parts of both planum tectale and processus antorbitalis, the latter being beneath the foramen. The more dorsal posi-

tion of the antorbital in this stage, may be explained by the presence of the muscularis process of the quadrate, and its attachment to the planum basale just ventral to the antorbital (Fig. 83).

Just in front of the choana, which opens into the mouth slightly anterior to the ethmoidal column, a longitudinal constriction of the nasal sac partially divides it into two chambers; one medial and dorsal, lying upon the lateral part of the trabecula, the other lateral and more ventral (it is the beginning of Jacobson's organ), which lies to the side of and to some extent beneath the trabecula.

The olfactory nerves of the two sides now pass from the forebrain forward and beneath the pons ethmoidalis to the nasal sac. Later, a chondrification ventral from the pons completely obliterates the fenestra ethmoidalis and, forming the ethmoidal wall, it outlines the two olfactory foramina in the anterior lateral angles of the cavum cranii.

Anterior to the planum basale, the trabeculae diverge, enclosing a wedge-shaped internasal space between them. At first more narrow, each trabecula widens nearer its tip; and, just in front of the level of the naris, bends abruptly downward to end near the inferior labial cartilage. This vertical portion of the trabecula is apparently what Gaupp calls the superior labial cartilage, and which he figures as a discrete element in both his earlier and later stages. I do not find in my material any line of demarcation between the trabeculae and the superior labial cartilages.

I have had no material intermediate between the larval stage just described and a young frog soon after metamorphosis. But it is easy to see, however, that the changes undergone are about as follows; this account agreeing substantially with that of Gaupp.

As in a larva of Bufo, a tadpole of Rana approaching the end of metamorphosis, according to Gaupp, shows a decided reduction in the sagittal plane of the anterior part of the nasal capsule. This reduction is caused by a partial resorption of the earlier larval trabeculae, so that the definite nasal capsule is formed by a development of the posterior parts of the trabeculae, together with certain independently chondrified parts.

Subsequent to the closure of the fenestra ethmoidalis, by the development of a perpendicular ethmoidal wall, the planum verticale chondrifies anteriorly, separating the nasal organs of the two sides and uniting the planum basale in its median line to the planum tectale, which has grown forward from the dorsal margin of the pons and the ethmoidal column. The lamina externa forms the side wall of the capsule, and develops from the lateral part of the tectale; it unites to the oblique cartilage, which chondrifies independently and lies diagonally across the nasal sac from the lamina externa to the more anterior tectale.

In the anterior part of the capsule, the greatest modification takes place. The loss of the labial cartilages and the anterior parts of the trabeculae

causes a shortening of the capsule, which is accompanied by an increase in its depth. In front, each trabecula gives rise to a solum anterius which forms the anterior wall of the capsule; and at its junction to the tectale each solum gives rise to an alinasal cartilage, which supports the anterior end of the nasal sac and forms the posterior boundary to the external naris. The large naso-basal fenestrae between the medial margins of the anterior walls of the capsule and the planum verticale open from the nasal cavity to the internasal space much as in Bufo.

In this stage, the articulation of the lower jaw has moved backward, so that the deeply curved muscularis process of the quadrate is more posterior; and, as a result, the pterygoid has united to the capsule at the point of origin of the tectale from the ethmoidal column, the anterior maxillary process reaching forward from the junction of the two.

In a young adult of *Rana viridescens* (Figs. 85, 86) there has been a relative reduction in the height of the verticale, although the proportion of breadth to length is approximately unchanged. Anterior to the cavum cranii, planum tectale, basale and verticale have fused into a thick plate, recalling the association of these same structures in Amblystoma. The olfactory foramen (*fo*) opens obliquely forward from the antero-lateral angle of the cavum cranii to the nasal cavity just beneath the foramen orbito-nasalis the posterior opening of which lies adjacent to the lateral margin of the cranial wall. Lateral to the foramen orbito-nasalis, the fused tectale and antorbital curve outward and downward over the choana and continue posteriorly into the pterygoid, while anteriorly a small maxillary process reaches forward midway to the tip of the capsule.

The nasal sac is completely covered dorsally by the lateral parts of the planum tectale which reaches forward to the tip of the cranium, and is considerably narrower at the anterior end. At about the middle of the tectale, an oblique cartilage bar (*oc*) extends backward and slightly outward, ending bluntly near the anterior end of the maxillary process (*amp*). Although unconnected in this stage, these two structures are probably the homologue of the lamina externa and the oblique cartilage of the larva.

The nasal sac opens to the exterior just anterior to the oblique cartilage, where the alinasal cartilage, continuous anteriorly into a superior prenasal, forms the floor of the naris. Beneath the alinasal, but connected to it, is a thick cartilage, the crista subnasalis (*cr s*) possibly a remnant of the earlier solum anterius, although evidence is lacking here. Anterior to the crista sub-nasalis is the inferior prenasal process, which extends ventrally from the capsule; while directly above it is the fenestra naso-basalis, greatly reduced here, and more like that in Hyla.

COMPARISON OF THE NASAL CAPSULES IN THE ANURA

The division of the Anura into the suborders Aglossa and Phaneroglossa is borne out by this study of the nasal capsules; for Pipa would appear to be far removed from the other Anura, and because of the large vacuities in the chondrocranium it may be said to be more like the Urodeles.

In all of the Anura, the extension of the pterygoid process to the nasal capsule is the normal condition, and recalls this relationship in Cryptobranchus Furthermore, the planum tectale, apparently a lateral growth from the. columna ethmoidalis, unites to the pterygoid, the two forming in Bufo the lamina externa, which forms the side wall of the capsule; while in the adult Rana, the anterior connection of the lamina externa is lost, the united pterygoid and tectale forming the anterior maxillary process.

The cavum cranii of Pipa is not as well developed as in other Anura, the alisphenoids being but little higher than the planum basale, and less crest-like in their appearance. The forebrain in Pipa lies dorsal to the posterior part of the nasal sac, rather than posterior to it as in Bufo; and, if the olfactory nerve may be regarded as sufficient evidence for the determination of homologies, then that part of the basale in Pipa, anterior to the foramen olfactorius, must be the perpendicular ethmoidal wall in Bufo and other Phaneroglossa. This change in the relative position of these parts may be explained by the statement of Gaupp that the chondrocrania of larvae of *Rana fusca* suffer a reduction in the sagittal plane during metamorphosis.

In both groups, the roof of the capsule, anterior to the region just described is formed by a fusion in the middle line of the ethmoidal columns, which also unite to the planum verticale. In Bufo, the extent of the tectale lateral to the verticale is considerably more than in Pipa, where the medial parts of each nasal sac are but slightly covered and suggest for Pipa a more complete fusion of the ethmoidal columns. There is no floor of the nasal capsule in Pipa, while in all the Phaneroglossa the planum basale extends forward from the cavum cranii to the tip of the capsule, where each lateral angle expands into the alinasal cartilage. The presence of these alinasals in Pipa would suggest that the ventral half of the planum verticale must be a fused and greatly reduced trabecular plate, homologous to the anterior planum basale in the Phaneroglossa.

The lateral wing of the capsule, the so-called ethmo-palatine of Parker or planum terminale of Gaupp, but more properly designated the lamina externa in Bufo, is formed, partly from the pterygoid and partly from the columna ethmoidalis. In both groups two cartilage bars unite the lamina

externa to other parts of the capsule; although differing in their relations to each other, and in their position in the capsule, their homology is very evident. The ventral of these two bars is the cornu trabecula, more slender and cylindrical in Pipa; while in Bufo it is greatly reduced in length, considerably broader and has been designated in this paper as the solum anterius. The junction in both groups of this cartilage with the alinasal cartilage is a further evidence of their homology. The dorsal of the two bars, above mentioned, is apparently an additional structure in the Anura, for I do not recognize it in any Urodele. The term oblique cartilage seems to best designate this bar, extending, as it does, obliquely forwards and upwards from the lamina externa to the planum tectale, or as in Pipa to the tip of the planum verticale.

CONCLUSIONS BASED ON THIS STUDY

PHYLOGENY OF THE NASAL CAPSULE IN AMPHIBIA

The cartilaginous nasal capsule of Amphibia must have been derived from that of some lower vertebrate, be it Dipnoan or be it Crossopterygian, and that in turn from the Elasmobranch. So far as our knowledge goes, the Elasmobranch capsule is a continuous cartilaginous structure with no gaps or openings except that for the naris and the small foramina for the passage of nerves. The amphibian capsule, on the other hand, has interruptions in its walls; some of which are due to the fact that in the adult, bones appear in the nasal region and thus do away with the necessity of the persistence of protecting cartilages in certain places. Some are caused by the development of a complete olfactory duct with its choana, in addition to the naris.

Within the class of Amphibia there are many differences between the various capsules, caused by differences in the size and shape of the covering bones, by the changes in the development and shape of the organ of Jacobson, the modifications of the lacrimal duct, as well as by the difference in the size and shape of the olfactory sac. It follows, therefore, that in the history of the amphibian capsule, two stages should be recognized; one a progressive process in which the capsule is built up, a repetition of the ancestral (piscine) history, and the other in which this capsule is reduced and changed into the definitive form.

In following these two stages, we are hampered in our conclusions by the fact that we have no accurate and detailed account of the development of the capsule of any fish, and expecially in those groups universally recognized as ancestral. Neither Parker nor Sewertzow give any details of the development of the Elasmobranch capsule which can be used in this connection. The studies made in this laboratory of the development of the capsule in Acanthais only go far enough to show that it consists, when it first is recognizable, of a rudimentary floor, and an even more incomplete roof, and that these arise independently of the trabeculae or other cranial elements.

The foregoing studies show, that in those forms where the development has been followed with any detail from one stage to another, that there is first a progressive development, apparently tending toward the formation of a complete capsule like that of the adult Elasmobranch. Then alterations occur, largely degenerative in character, which result in the partial reduction of the floor and roof. These progressive changes

are well exemplified in Necturus where, even in the adult, the capsule is more nearly entire than in any other genus; a condition which may be explained on the supposition that Necturus is to be regarded, not as more primitive than other Urodelan genera, but as a permanent larva, a view which has been advocated by many in recent years.

In Amblystoma, as detailed in the foregoing pages, this history is carried farther. There is first a progressive development tending toward a complete capsule, but never approaching completeness as nearly as does the adult Necturus. Then, in conjunction with the process of metamorphosis, there comes a resorption of parts and a modification of those that persist, resulting in large vacuities in both floor and roof of the capsule. These steps are detailed above, and the final result is an envelope for the olfactory organ in which parts are recognizable as homologous with those of the capsules of the adult Anura.

In the history of the capsules in all Amphibia the following parts are concerned. The two trabeculae are united in the 'ethmoid' region by what Gaupp and others have called an internasal plate. This lies below the tip of the brain and is the 'ethmoid plate' of Winslow or the 'planum basale' of the foregoing description. In front of this planum basale, the trabeculae continue as the cornua trabeculorum to the tip of the skull, supporting the anterior part of the nasal organ. In several Urodeles, where I have studied the early larval stages (this history has not been followed in the Anura with sufficient detail to say whether it holds for them) a bar of cartilage, the columna ethmoidalis, arises on the upper medial side of the olfactory organ (either independently or as an outgrowth from the cornu) and lies parallel to the lower trabecula. By a lateral growth from this ethmoidal column, the planum tectale extends over the dorsal surface of the nasal sac, uniting in the later stages to the cornu trabeculae. The term lamina cribosa, used by Winslow (1898) and Terry (1906) to designate this cartilage is a misnomer, for it is hardly necessary to say that it cannot be homologous with the structure bearing the same name in the mammals, as it lies wholly dorsal to the olfactory nerve.

In the larvae of several Urodeles, and in my single larva of Rana, the ethmoidal columns of the two sides are connected by a pons ethmoidalis which roofs the fenestra ethmoidalis leading from the cavum cranii to the ethmoid region. This is only a temporary condition in most amphibia where the chondrification of the planum verticale closes the fenestra and unites the floor and roof of the capsule. In Triton and Diemictylus, on the other hand, the planum verticale never develops; so that cavum cranii and internasal space are separated by membranous structures only.

The last special element entering into the formation of the capsule is the antorbital process, which needs a somewhat longer discussion. In the Urodeles, a process arises from the side of the trabecula just back of

the choanal region; it extends laterally a short distance, then turns forward and later uniting to the planum tectale forms a part of the lateral wall and floor of the capsule. This has almost universally been called the antorbital process; but the larva of Cryptobranchus shows what it really is. In my second larva of this animal the pterygo-quadrate bar extends forward from the hinge of the lower jaw and joins the trabecula at the same point from which the antorbital projects in other Urodeles. In Ranodon judging from Wiedersheim's figure (1877, Fig. 69), there is a similar connection of the pterygoquadrate with the anterior part of the skull. Elsewhere in all described Urodeles, as far as I have been able to discover, there is only an extension of the pterygoid process forward from the quadrate towards the capsular region; and even in the adult Cryptobranchus (and this holds also for the Japanese species, as figured by Parker) the connection between the pterygoid and the structures farther forward is lost.

In all the Anura, on the other hand, the pterygoid cartilage is connected throughout life with the nasal capsules. In this respect Ranodon, and to a less degree Cryptobranchus, approach the Anura more closely than any of the other Urodeles. It is usual to regard this arch as the homologue of the upper jaw of the Elasmobranch, which, with the development of the osseous upper jaw of the Teleostomes and higher groups, has lost its original function as a part of the feeding apparatus, and has fused with the side of the cranium, its middle portion dropping out in the process. It may be remarked parenthetically, that the name palato-quadrate commonly given this arch is incorrect, as it contains no palatal element and no part of the palatine bone is developed from it.

In no Elasmobranch is there any extension of the pterygoid as a distinct process beyond the curve of the arch of the upper jaw. On the other hand, in all of the Amphibia there is such a forwardly directed process, the antorbital, already referred to. It would then apparently follow that the antorbital process of the Urodele, is in its basal part, the anterior end of the pterygoquadrate, while its anterior portion is a new formation. That this interpretation is correct, is supported by all of the Anura that I have studied.

In my earlier stages of Salamandra (in which there is no connection at any stage between the pterygoid process and the structures farther forward) the antorbital process is developed and extends forward beneath the nasal capsule; but as yet it is unconnected distally with any other cartilage. Just dorsal to the base of this process, both the ophthalmic and superficialis branches of the fifth nerve pass into the capsular region. Thus the antorbital process is ventral to these nerves. In the oldest larva that I have of this genus, the roof of the capsule (planum tectale) has extended back so that its posterior margin overlies the base of the antorbital, while between the tectale and the antorbital there is a very large gap.

In other genera, both Urodele and Anuran, these same nerves pass through a small foramen in the region corresponding to that in Salamandra; and since nerves and their distribution may be regarded as sufficient criteria, it follows that this part of the capsule is a composite of a ventral antorbital and a dorsal tectale.

In Pipa, Bufo and Rana, the pterygoid joins the side of the anterior part of the cranium, this distal portion being nearly at right angles with the axis of the skull. At the anterior side, a process extends forward from the bend in the pterygoid, forming the postero-lateral wall of the capsule. This is the lamina externa in Bufo and Hyla; and in the adult Rana, where its anterior connection with the capsule has been lost, the lamina externa becomes the anterior maxillary process. This anterior process, then, reaching forward from the pterygoid, be it ethmo-palatine (Parker 1881) or planum terminale (Gaupp, 1893) can be none other than the antorbital process of the Urodeles; and it is joined either in front (Bufo and Rana) or upon its ventral surface (Pipa) by two cartilages, the oblique cartilage bar and the cornu trabeculae, the latter being designated the solum anterius in the Phaneroglossa.

On the basis of the nasal capsule, Epicrium is far removed from either the Urodeles or the Anura; and it would appear that the grouping of the recent Amphibia into three orders by Müller (1832) is borne out by this study. Anterior parts of a pterygoid reach well forward into the nasal region, and although there is no continuity between the pterygoid and the antorbital (which in my material has united to the more anterior parts of the capsule); yet a sharp process extending from the latter toward the pterygoid leads to the assumption that at one time these parts were continuous and that the antorbital process in Epicrium has had a pterygoidal ancestry.

CLASSIFICATION OF THE AMPHIBIA

The earliest classification of the Amphibia did not include the extinct with recent forms, largely because of the uncertainty of the systematic position of the fossil forms, which were regarded by some as reptiles. It was not until 1854 that Vogt stated that Archeosaurus and all the Labyrinthodontia are amphibians and not reptiles. Owen (1866) was among the first to propose a classification to include both extinct and recent forms.

Since these earlier days most Zoologists divide the class into four orders: namely; the Anura, Urodela, Gymnophiona and Stegocephala. There have been few variations in the subdivisions in the Anura and the Gymnophiona, but with regard to the Urodeles ideas have differed greatly. Some would recognize only Salamandrina and Ichthyoidea; while more commonly the tendency has been to subdivide the group into Perenni-

branchs, Derotremes and Salamandroidia,[1] according as external gills persist through life, as gill clefts remain permanently open or, in the latter, as the animals undergo a complete metamorphosis, losing their external gills and gill-clefts.

Strauch (1870) divided the Urodeles into two sub-orders, the Salamandrida and the Ichthyoidea. The basis of his classification was the presence or the absence of eyelids, the arrangement of the palatal teeth, and the permanence of gills and gill clefts. The Salamandrida were subdivided into two groups according to the arrangement of the palatal teeth. Those Urodeles in which these teeth formed diverging rows upon the inner margin of the palatine were grouped as the Mecodonta; while the Lechriodonta included those animals in which the palatal teeth form converging rows along the posterior margin of the palatine. The Mecodonta embrace six genera of which Salamandra, Triton and Diemictylus are represented in this paper; while of the thirteen genera included in Strauch's Lechriodonta, I have studied Amblystoma, Plethodon and Spelerpes.

The Ichthyoidea are divided into two groups, the Cryptobranchiata and the Phanerobranchiata, according to the persistence of gill clefts only or of both gills and gill clefts. Cryptobranchus, Menopoma and Amphiuma belong to the former group; while Necturus, Proteus and Siren are included in the latter.

The nasal capsules would support a classification of the Urodeles similar to that of Strauch. In the fore-going pages, I have included Spelerpes, Plethodon and Amblystoma (part of the Lechriodonta of Strauch) in a group descended from the more primitive Cryptobranchus; while Salamandra, Triton and Diemictylus (the Mecodonta of Strauch) are included in a group connected with the other group through some form like Spelerpes. I have regarded Cryptobranchus as more primitive, and Amphiuma as closely related to it, although not in the main line of descent. Strauch has grouped Necturus and Proteus into the Phanerobranchiata more distantly related to Cryptobranchus, while I have regarded Necturus as a permanent larva of some Spelerpes-like animal. I have not studied Proteus, but have placed Necturus in a separate group in keeping with the later Perennibranchiate classification.

Accordingly on the basis of the nasal capsules, I would adhere to the classification of the Urodeles into three suborders, the Perennibranchiata [Phanerobranchiata (Strauch)], the Derotrema [Cryptobranchiata (Strauch)] and the Salamandroidia. The latter may be divided into two groups, and, following Strauch, the terms Mecodonta and Lechriodonta may be retained.

[1] In many text books, this is given as Salamandrina, but the group was called Salamandroidia by Fitzinger (1826) who in the same place describes a genus Salamandrina. Confusion is therefore avoided by restricting the latter name to the genus while Salamandroidia with its ordinal termination may be retained for the larger group.

Cope (1889) misled by a supposed ethmoid bone in Amphiuma placed the Caecilians with the Urodeles, in which view he was later supported by the Sarasins (1890). Kingsley (1902) definitely determined the position of the Caecilians and maintained Huxley's conclusion that the Gymnophiona have probably separated from the ancestral Amphibia back in the early Carboniferous period. The nasal capsule of Epicrium is further evidence of the wide divergence of this group from all other Amphibia.

The Anura are readily separated into two groups, on the basis of the nasal skeletons, and these agree with the extablished classification into the Aglossa and the Phaneroglossa. Cope's subdivision of the latter into Arcifera and Firmisternia is not so readily recognized in the nasal capsules of my material, although there are more resemblances between the capsules of Bufo and Hyla, than of either with that of Rana.

AMPHIBIAN ANCESTRY

The Amphibians appear, as Stegocephals, in the Carboniferous period, and although from the first they are considerably diversified, there is not known a single trace of any tetrapodous vertebrate in the Devonian with the sole exception of a single footprint from the Pennsylvanian. In the Devonian and somewhat earlier, fishes belonging both to the Dipnoi and to the Crossopterygian ganoids occur, and both of these piscine groups have been invoked by various zoologists as the ancestors of the Amphibia, possibly the tendency of the evidence at present favoring the Crossopterygians.

All of the amphibians of the Carboniferous, with the possible exception of Pelion, were caudate. Moodie (1916), the latest to study these ancient forms, is inclined to regard Micrerpeton, a small Salamandra-like form, as representing the ancestors of the modern groups, with Necturus as an annectant genus. He bases this conclusion upon the resemblances of the skull, the form of vertebrae and ribs, the peculiarities of the lateral line system, and the presence in both of 'ventral scutellations,' a view which closely resembles the earlier ideas of Cope.

But it would seem as if Moodie was leaning upon a weak reed in invoking ventral scutellations as an argument, no matter what view one may take with regard to the other points of resemblance. It is well known that many of the Stegocephals had ventral scutes, plates or bars upon the ventral surface of the body, but the universal view is, that these structures were purely dermal, belonging like scales of fishes to the skin. Moodie cites Wilder as stating that Necturus had small cartilages in the ventral region, and apparently he regards these as the homologue of the ventral armor of Stegocephals. But there are very important differences between the two.

Most students have regarded the gastralia of Sphenodon and the Crocodilia as derivatives from the plates and bars of the Stegocephals. These latter are also suggested as forming the elements from which the clavicles and episterna of the higher vertebrates are derived. In Sphenodon, according to Osawa (1896) and Howes and Swinnerton (1901), the gastralia develop without any cartilage basis, and, with the single exception of Schneider, no one has ascribed any cartilage stage for the gastralia of the alligators and crocodiles; while Voeltzkow and Döderlein (1901) shows that in Crocodiles there is no cartilage stage in these structures. In short, the great bulk of the evidence goes to show that these so-called abdominal ribs are dermal elements without any cartilage stage.

Wilder explicitly states that the cartilages he describes in the ventral surface of Necturus lie in the myocommata; that is, entirely deeper than the skin. He compares them to sternal elements. Hence it would appear that other evidence than these intermuscular cartilages must be brought forward to support his thesis.

According to Moodie, Micrerpeton has well developed nasals, prefrontals and elongate maxillaries, all of which are lacking in Necturus. Now if Necturus is to represent the ancestors of the modern Urodeles in which these same elements are present, we have the difficulty of explaining how these bones disappeared from the line of descent and then were reformed in the later generations.

Cope regarded Necturus as primitive because it possessed what he called an intercalary bone in the skull, an element which he also recognized in the Stegocephals. But Kingsbury (1905) says, that, at least in Necturus, Cope's intercalary was the caudal extension of the opisthotic.

Nothing is known of the cartilaginous nasal capsules of the Stegocephala, so that no comparison can be made between those of Necturus, and Micrerpeton. However, the complete isolation of the Necturan capsule and its wide separation from that of the other Urodeles, is certainly one argument against the ancestral position of this animal. Furthermore, the absence of maxillaries, nasals, and prefrontals in Necturus is one of the arguments of Kingsbury (1905) in regarding Necturus as a permanent larva, a conclusion which a study of the nasal capsule suggests.

Moodie (1916, p. 24) says: "The condition found in the skull of Cryptobranchus alleghaniensis will represent pretty accurately the condition of most of the coal measures Amphibia." Farther than this no emphasis is laid upon the primitive condition of Cryptobranchus. However, because of the simplicity of the nasal capsule, the persistence of the pterygoquadrate arch, and also because of the time and manner of the ossification of the skull, I am inclined to regard Cryptobranchus as more primitive.

As a study of the nasal capsules suggests, the Urodeles are widely separated from the Anura. Fossil Anura occur in an excellent state of

preservation as far back as the Tertiary. Earlier than this all known fossil forms are caudate, with the exception of a single specimen, Pelion lyelli, found in the Carboniferous, which closely resembles recent Salientia. Should Pelion prove to be a primitive Anuran, then the Urodeles and the Anura have probably separated from the Stegocephalan ancestor as far back as the late Devonian or early Carboniferous period.

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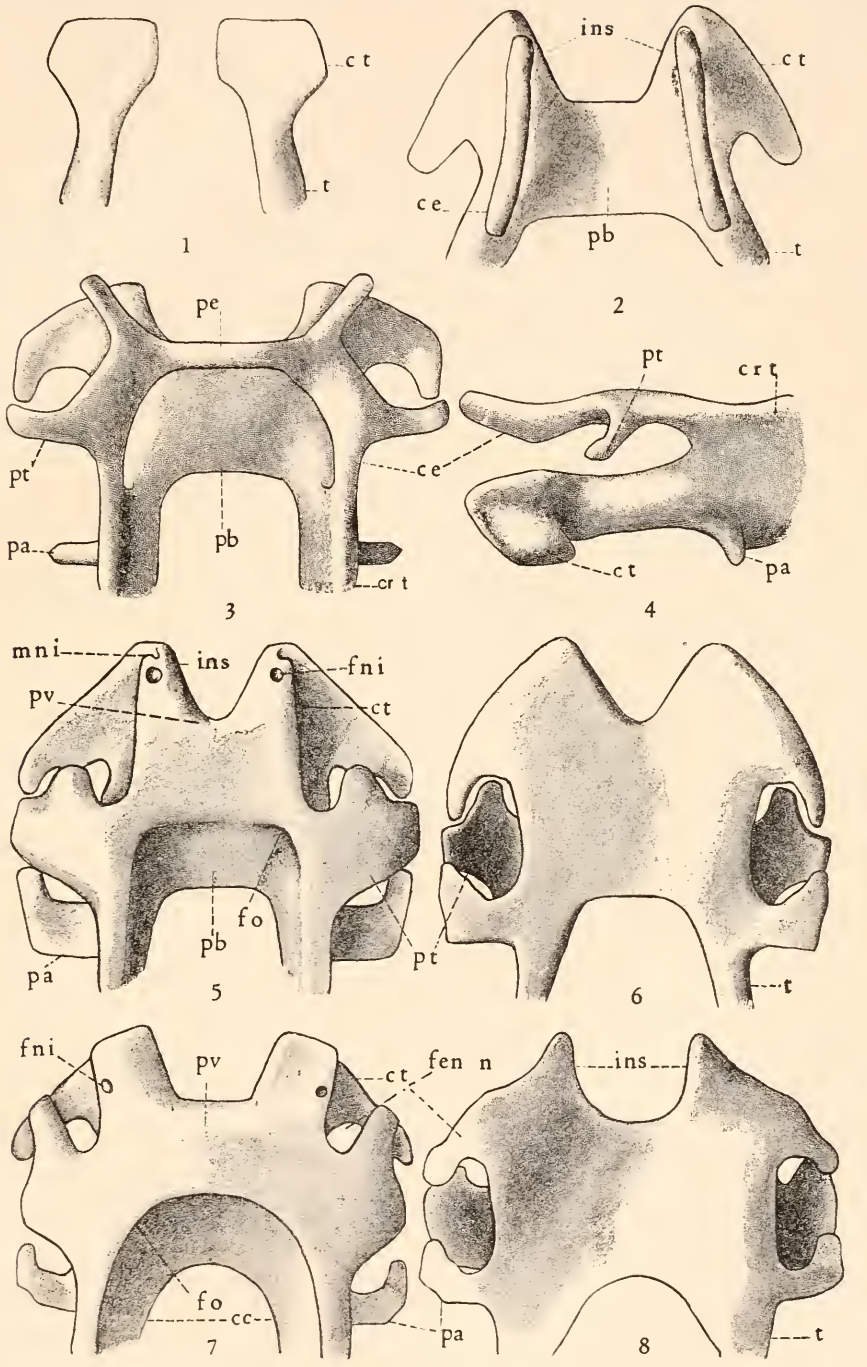
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PLATE I

EXPLANATION OF PLATE

Fig. 1.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 11 mm. long.
Fig. 2.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 20 mm. long.
Fig. 3.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 25 mm. long.
Fig. 4.—Side view of model of nasal capsule of *Amblystoma punctatum* 25 mm. long.
Fig. 5.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 34 mm. long.
Fig. 6.—Ventral view of model of nasal capsule of *Amblystoma punctatum* 34 mm. long.
Fig. 7.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 45 mm. long.
Fig. 8.—Ventral view of model of nasal capsule of *Amblystoma punctatum* 45 mm. long.

ce	columna ethmoidalis	*mni*	median nasal incisure
cr t	crista trabeculae	*pa*	processus antorbitalis
ct	cornu trabeculae	*pb*	planum basale
fen n	fenestra narina	*pe*	pons ethmoidalis
fni	foramen nasalis internus	*pt*	planum tectale
fo	foramen olfactorius	*pv*	planum verticale
ins	internasal space	*t*	trabecula



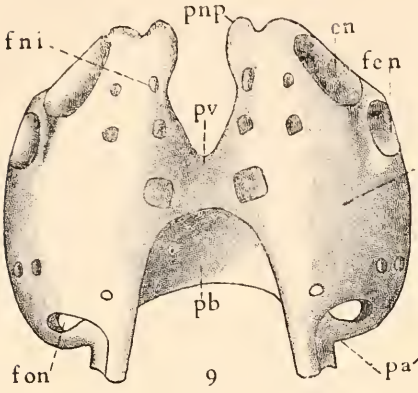
HIGGINS NASAL ORGAN IN AMPHIBIA PLATE I

PLATE II

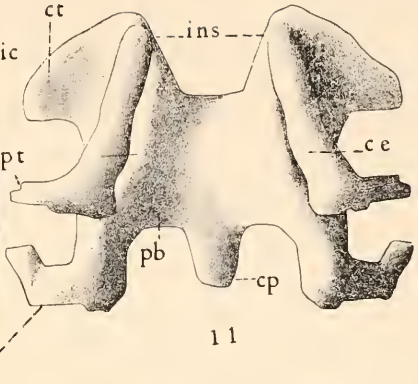
EXPLANATION OF PLATE

Fig. 9.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 55 mm. long.
Fig. 10.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* at the end of metamorphosis.
Fig. 11.—Dorsal view of model of nasal capsule of *Salamandra maculata* 25 mm. long.
Fig. 12.—Dorsal view of model of nasal capsule of *Salamandra maculata* 38 mm. long.
Fig. 13.—Dorsal view of model of nasal capsule of *Salamandra maculata* at the end of metamorphosis.
Fig. 14.—Dorsal view of model of nasal capsule of *Diemictylus viridescens* 38 mm. long.

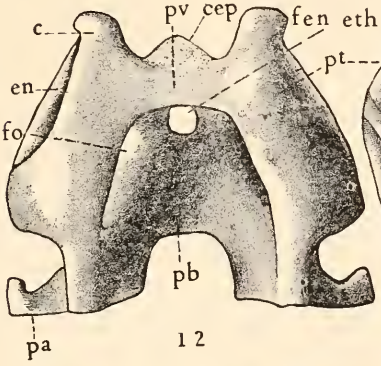
c	cupola	*fo*	foramen olfactorius
cc	cavum cranii	*fon*	foramen orbito-nasalis
ce	columna ethmoidalis	*ins*	internasal space
ce p	cephalic process	*le*	lamina externa
cp	caudal process	*lm*	lamina medialis
ct	cornu trabeculae	*pa*	processus antorbitalis
en	external naris	*pb*	planum basale
fen eth	fenestra ethmoidalis	*pnp*	prenasal process
fen ic	fenestra infra-conchalis	*pt*	planum tectale
fne	foramen nasalis externus	*pv*	planum verticale
fni	foramen nasalis internus		



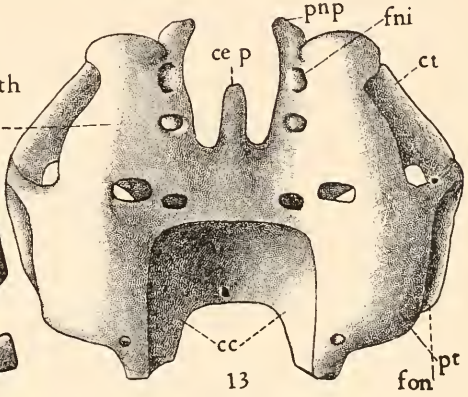
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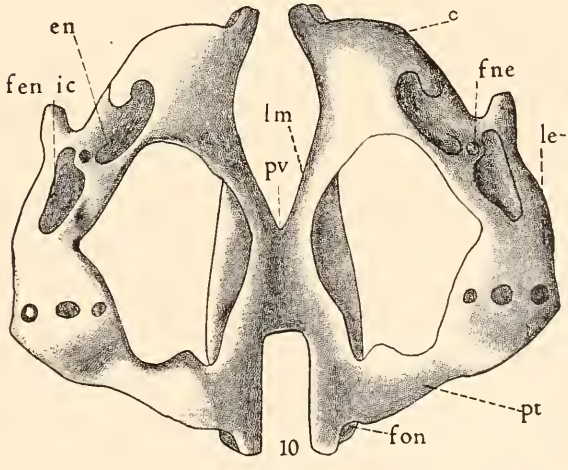
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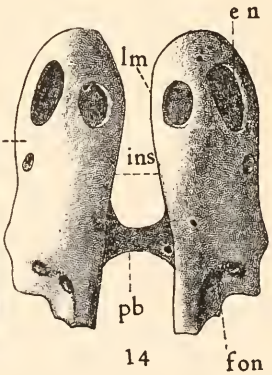
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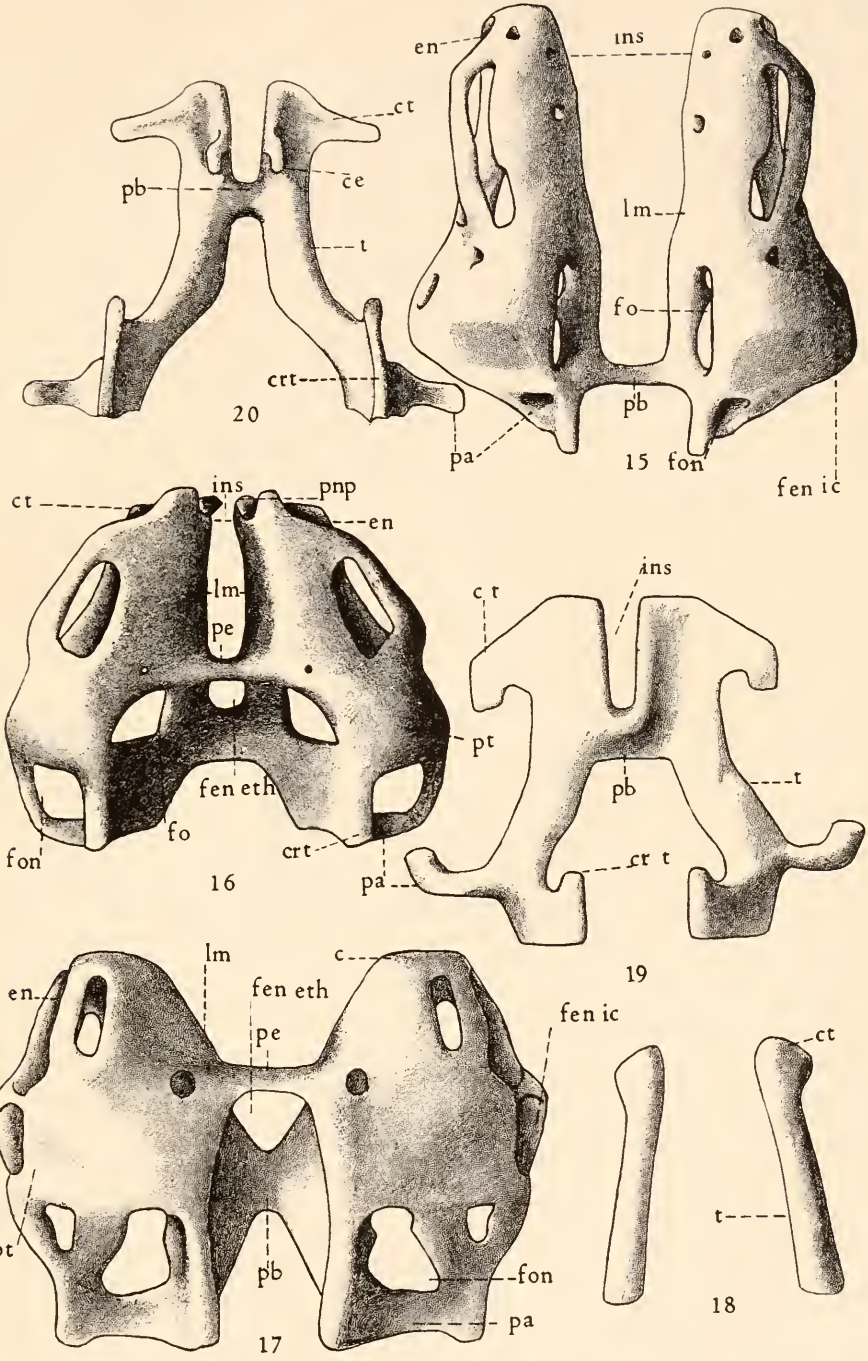
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PLATE III

EXPLANATION OF PLATE

Fig. 15.—Dorsal view of model of nasal capsule of an adult *Diemictylus viridescens*.
Fig. 16.—Dorsal view of model of nasal capsule of *Triton cristatus* 28 mm. long.
Fig. 17.—Dorsal view of model of nasal capsule of *Triton cristatus* 35 mm. long.
Fig. 18.—Dorsal view of model of nasal capsule of *Spelerpes bilineatus* 15 mm. long.
Fig. 19.—Dorsal view of model of nasal capsule of *Spelerpes bilineatus* 37 mm. long.
Fig. 20.—Dorsal view of model of nasal capsule of *Spelerpes bilineatus* 46 mm. long.

c	cupola
ee	columna ethmoidalis
cr t	crista trabeculae
ct	cornu trabeculae
cn	external naris
fen eth	fenestra ethmoidalis
fen ic	fenestra infra-conchalis
fo	foramen olfactorius
fon	foramen orbito-nasalis
ins	internasal space
lm	lamina medialis
pa	processus antorbitalis
pb	planum basale
pe	pons ethmoidalis
pnp	prenasal process
pt	planum tectale
t	trabecula



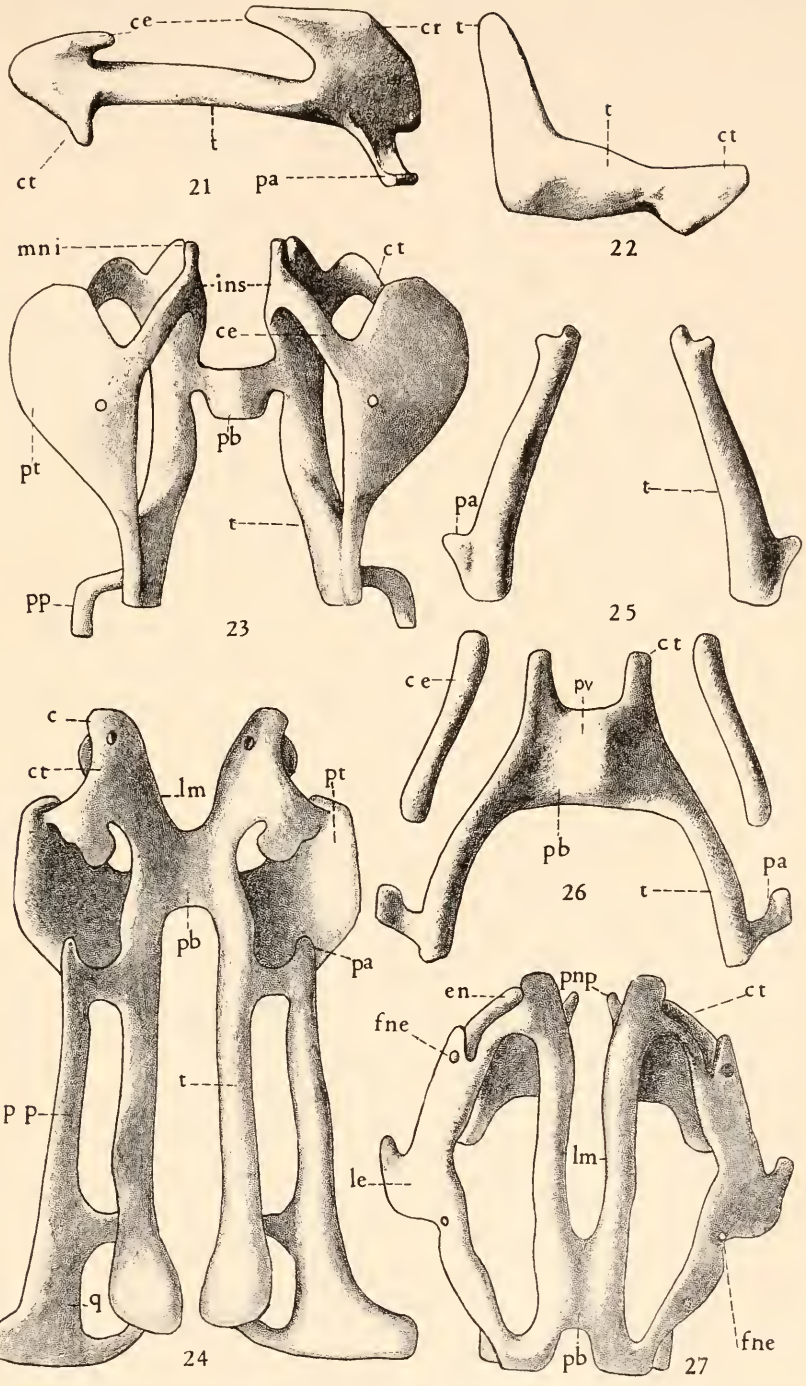
HIGGINS NASAL ORGAN IN AMPHIBIA PLATE III

PLATE IV

EXPLANATION OF PLATE

Fig. 21.—Side view of model of nasal capsule of *Spelerpes bilineatus* 46 mm. long.
Fig. 22.—Side view of model of nasal capsule of *Cryptobranchus alleghaniensis* two weeks old.
Fig. 23.—Dorsal view of model of nasal capsule of *Cryptobranchus alleghaniensis* five weeks old.
Fig. 24.—Ventral view of model of nasal capsule of *Cryptobranchus alleghaniensis* three months old.
Fig. 25.—Dorsal view of model of nasal capsule of *Necturus maculatus* 25 mm. long.
Fig. 26.—Dorsal view of model of nasal capsule of *Necturus maculatus* 30 mm. long.
Fig. 27.—Dorsal view of model of nasal capsule of a young adult of *Plethodon erythronotus*.

c	cupola	*mni*	median nasal incisure
ce	columna ethmoidalis	*pa*	processus antorbitalis
cr t	crista trabeculae	*pb*	planum basale
ct	cornu trabeculae	*pnp*	prenasal process
en	external naris	*pp*	pterygoid process
fne	foramen nasalis externus	*pt*	planum tectale
ins	internasal space	*pv*	planum verticale
le	lamina externa	*q*	quadrate
lm	lamina medialis	*t*	trabecula



HIGGINS NASAL ORGAN IN AMPHIBIA PLATE IV

PLATE V

EXPLANATION OF PLATE

Fig. 28.—Dorsal view of model of nasal capsule of *Necturus maculatus* 45 mm. long.
Fig. 29.—Dorsal view of model of nasal capsule of a young larva of *Amphiuma means*.
Fig. 30.—Ventral view of model of nasal capsule of an older larva of *Amphiuma means*.
Fig. 31.—Dorsal view of model of nasal capsule of *Amphiuma means* 82 mm. long.
Fig. 32.—Dorsal view of model of nasal capsule of a young larva of *Epicrium glutinosum*.
Fig. 33.—Dorsal view of model of nasal capsule of *Epicrium glutinosum* 90 mm. long.

al p	alary process
c	cupola
ce	columna ethmoidalis
ce p	cephalic process
ch	choana
cr	circumnarial ring
cr t	crista trabeculae
ct	cornu trabeculae
en	external naris
fen pr	fenestrated process
fne	foramen nasalis externus
fon	foramen orbito-nasalis
ins	internasal space
le	lamina externa
pa	processus antorbitalis
pb	planum basale
pob	preorbital band
pp	pterygoid process
pv	planum verticale
t	trabecula

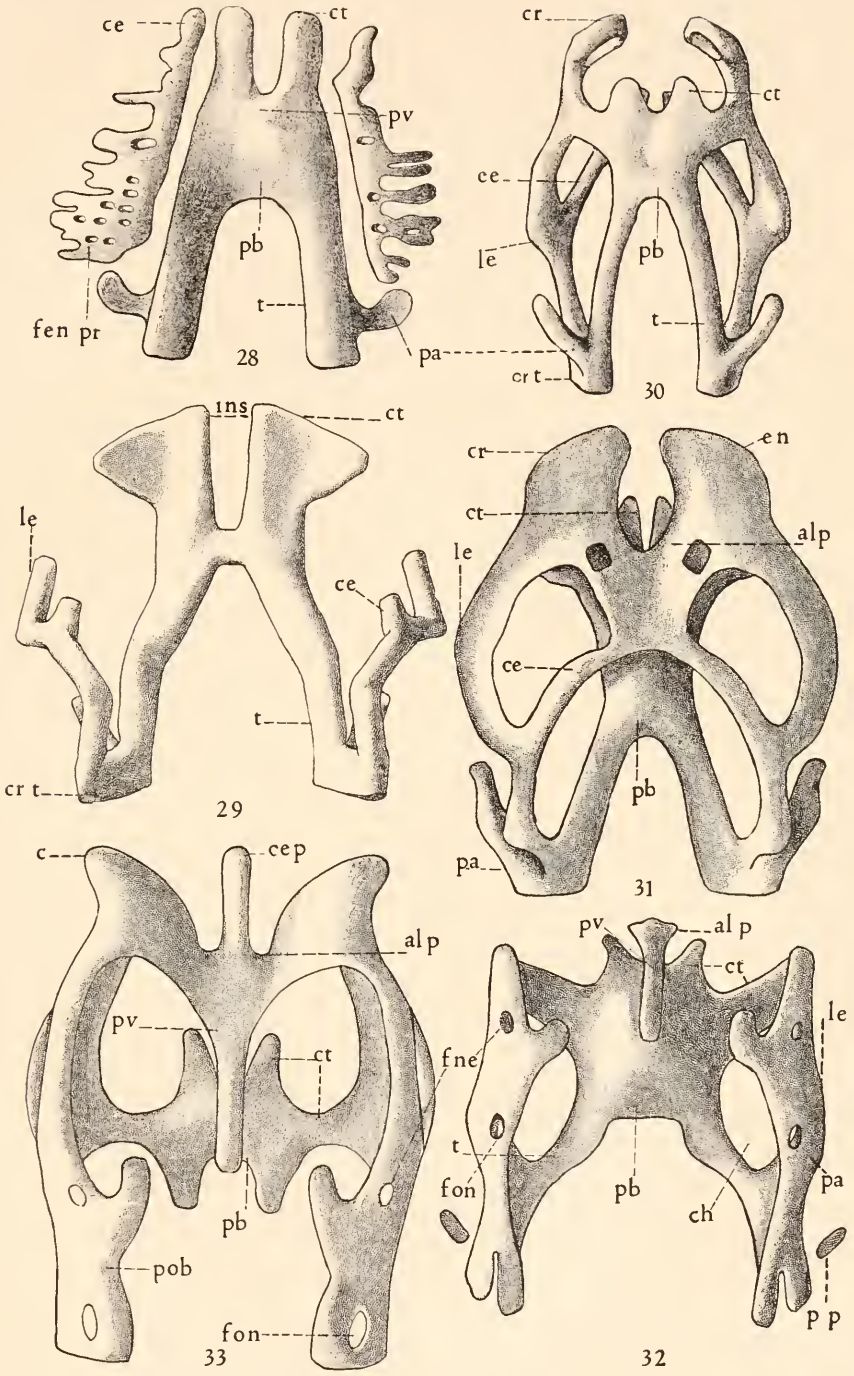
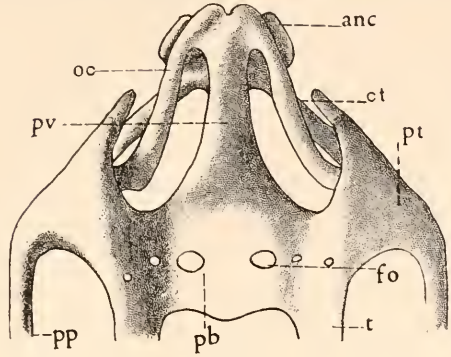

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PLATE VI

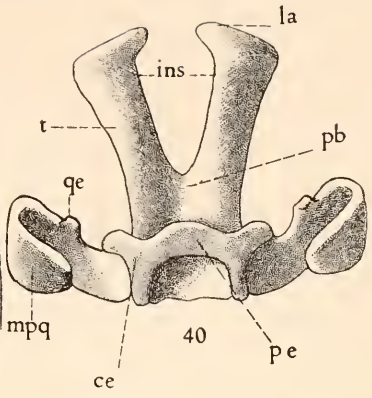
EXPLANATION OF PLATE

Fig. 34.—Dorsal view of model of nasal capsule of a young larva of *Pipa americana*.
Fig. 35.—Ventral view of the same model of *Pipa americana*.
Fig. 36.—Dorsal view of model of nasal capsule of *Bufo americana* 9 mm. body length.
Fig. 37.—Posterior view of anterior half of model of nasal capsule of *Bufo americana* 9 mm. body length.
Fig. 38.—Dorsal view of model of nasal capsule of the adult *Hyla pickeringii*.
Fig. 39.—Side view of model of nasal capsule of the adult *Hyla pickeringii*.
Fig. 40.—Dorsal view of model of nasal capsule of *Rana viridescens* 28 mm. total length.

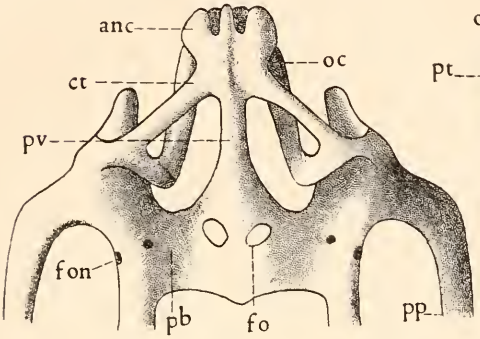
anc	alinasal cartilage	*la*	labial cartilage
ce	columna ethmoidalis	*le*	lamina externa
ci	cavum inferius	*mpq*	muscularis process of quadrate
cm	cavum medium	*oc*	oblique cartilage
cs	cavum superius	*pe*	pons ethmoidalis
ct	cornu trabeculae	*pb*	planum basale
en	external naris	*pp*	pterygoid process
fen nb	fenestra naso-basalis	*pt*	planum tectale
fni	foramen nasalis internus	*pv*	planum verticale
fo	foramen olfactorius	*qe*	quadrato-ethmoidalis process
fon	foramen orbito-nasalis	*sa*	solum anterius
ins	internasal space	*spc*	superior prenasal cartilage
ipc	inferior prenasal cartilage	*t*	trabecula



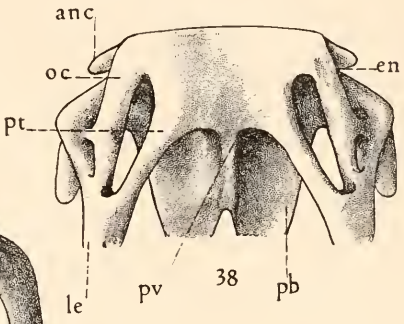
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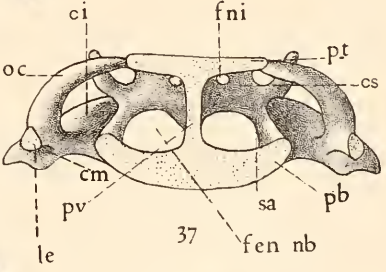
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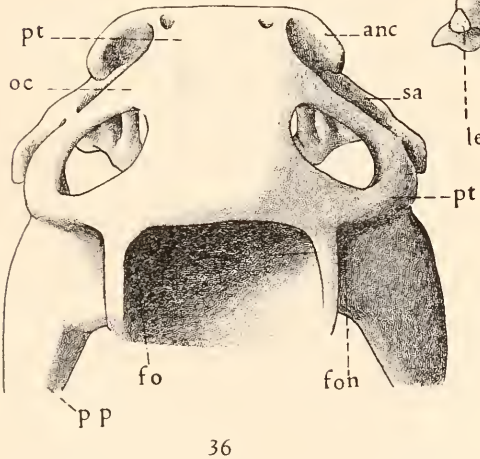
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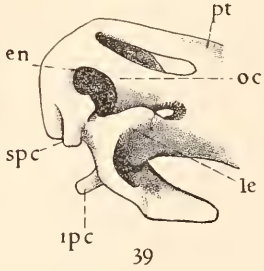
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PLATE VII

EXPLANATION OF PLATE

Fig. 41.—Transverse section through the anterior part of the nasal organ of *Amblystoma punctatum* 13 mm. long.

Fig. 42.—Transverse section through the middle region of the nasal organ of the same animal.

Fig. 43.—Transverse section through the choanal region of *Amblystoma punctatum* 20 mm. long.

Fig. 44.—Transverse section through the pons ethmoidalis of *Amblystoma punctatum* 25 mm. long.

Fig. 45.—Transverse section just anterior to the planum verticale of *Amblystoma punctatum* 55 mm. long.

Fig. 46.—Transverse section through the planum verticale of same animal.

Fig. 47.—Transverse section through the planum verticale of *Amblystoma punctatum* at the end of metamorphosis.

Fig. 48.—Transverse section through the lamina medialis of same animal.

Fig. 49.—Transverse section through the external naris of *Salamandra maculata* 25 mm. long.

Fig. 50.—Transverse section through the choana of the same animal.

Fig. 51.—Transverse section through the fenestra ethmoidalis of *Salamandra maculata* 38 mm. long.

Fig. 52.—Transverse section through the planum basale of *Salamandra maculata* at the end of metamorphosis.

cc	columna ethmoidalis	*ng*	nasal glands
ch	choana	*no*	nasal organ
ct	cornu trabeculae	*ol*	olfactory lobe
en	external naris	*p*	profundus branch of the fifth nerve
fen cth	fenestra ethmoidalis	*pa*	processus antorbitalis
fo	foramen olfactorius	*pb*	planum basale
ig	intermaxillary gland	*pe*	pons ethmoidalis
jg	glands of Jacobson	*pt*	planum tectale
jo	organ of Jacobson	*pv*	planum verticale
ld	lacrimal duct	*s*	superficialis of the fifth nerve
lm	lamina medialis	*t*	trabecula
le	lamina externa		

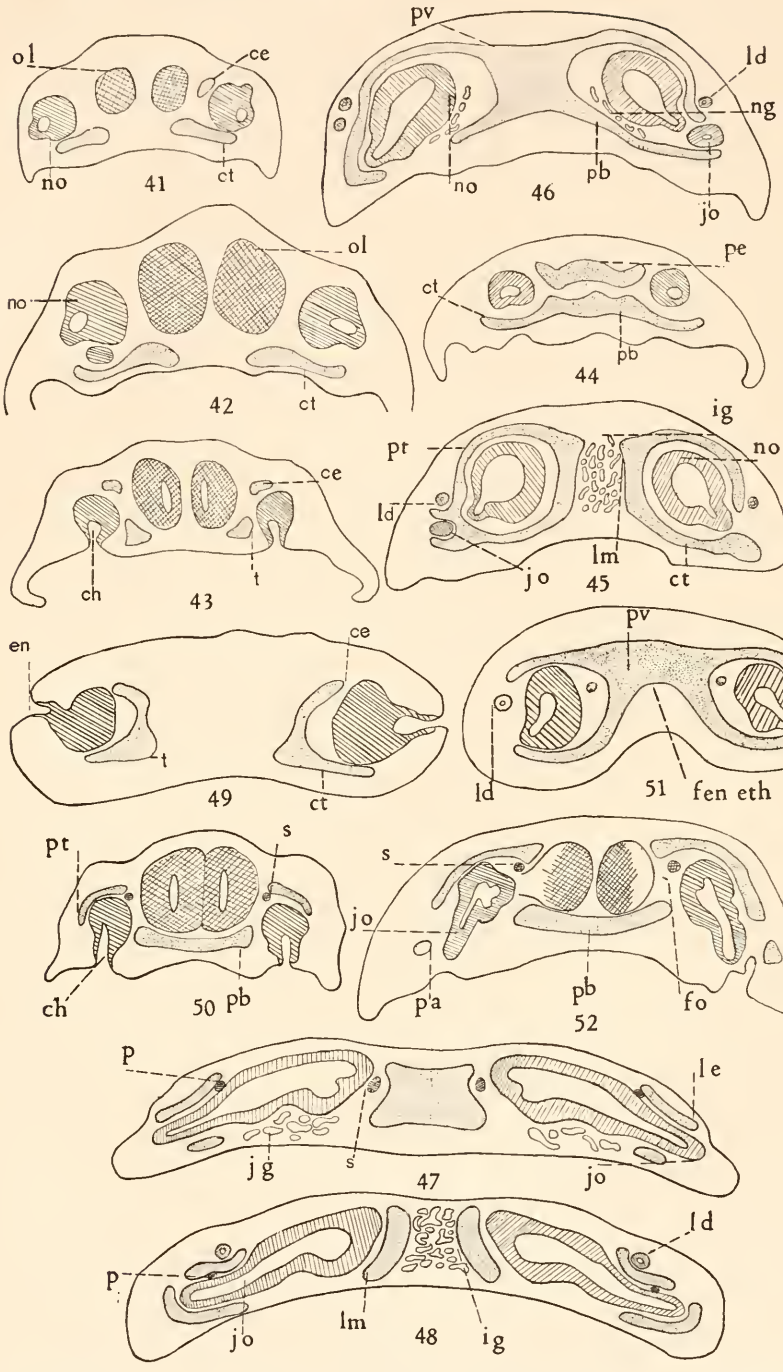

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PLATE VIII

EXPLANATION OF PLATE

Fig. 53.—Transverse section through the foramen olfactorius of *Diemictylus viridescens* 38 mm. long.

Fig. 54.—Transverse section through the anterior part of the nasal organ of the same animal.

Fig. 55.—Transverse section through the foramen olfactorius of the adult *Diemictylus viridescens.*

Fig. 56.—Transverse section through the pons ethmoidalis of *Triton cristatus* 28 mm. long.

Fig. 57.—Transverse section through the planum basale of *Triton cristatus* 35 mm. long.

Fig. 58.—Transverse section through the planum basale of *Cryptobranchus alleghaniensis* five weeks old.

Fig. 59.—Transverse section through the anterior end of the nasal organs of *Spelerpes bilineatus* 15 mm. long.

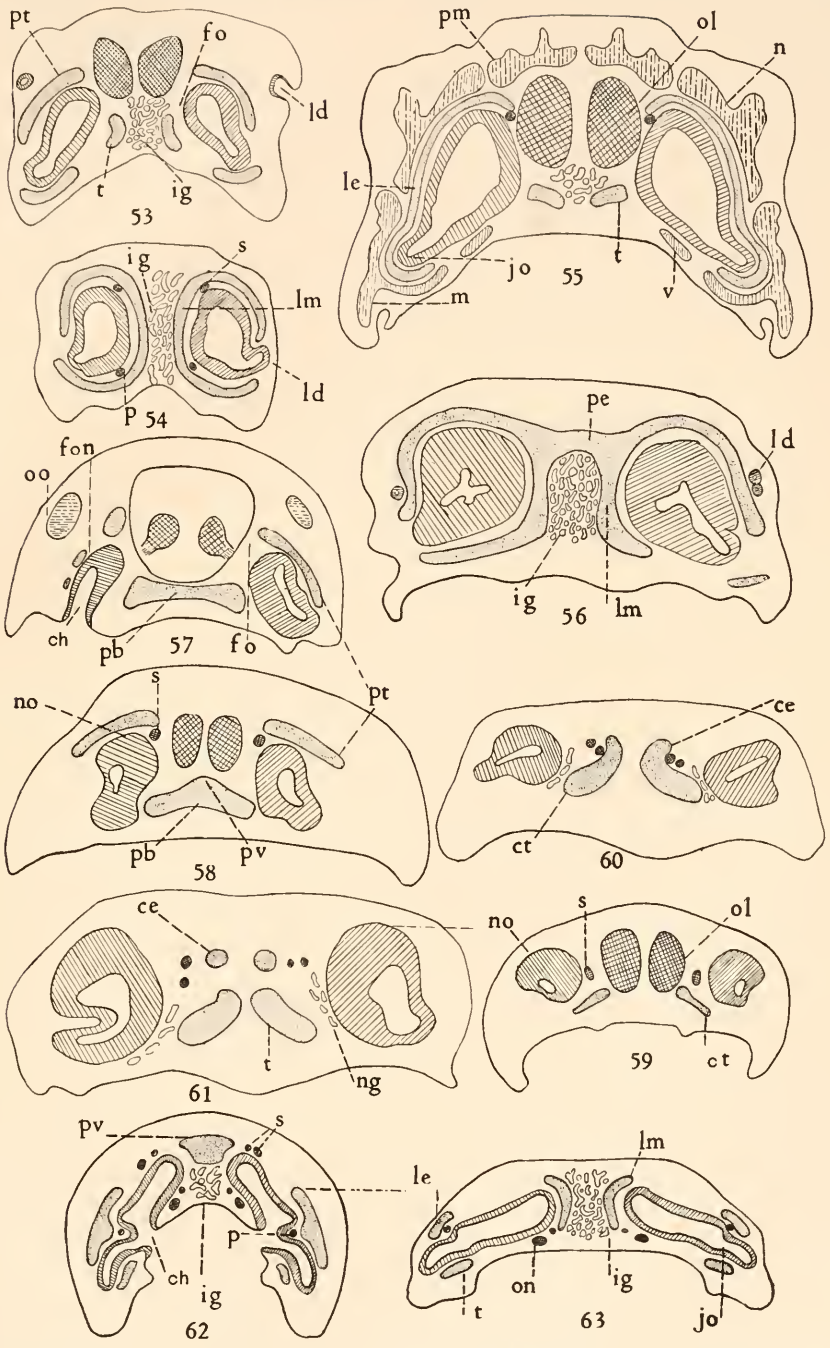
Fig. 60.—Transverse section just anterior to the planum basale of *Spelerpes bilineatus* 37 mm. long.

Fig. 61.—Transverse section through the same region of *Spelerpes bilineatus* 46 mm. long.

Fig. 62.—Transverse section through the choanal region of *Plethodon erythronotus* adult.

Fig. 63.—Transverse section through the lamina medialis of the same animal.

ce columna ethmoidalis
ch choana
ct cornu trabeculae
fo foramen olfactorius
fon foramen orbito-nasalis
ig intermaxillary gland
jo organ of Jacobson
ld lacrimal duct
le lamina externa
lm lamina medialis
m maxillary bone
n nasal bone
ng nasal glands
no nasal organ
ol olfactory lobe
on olfactory nerve
oo optic organ
p profundus of the fifth nerve
pb planum basale
pe pons ethmoidalis
pm premaxillary bone
pt planum tectale
pv planum verticale
s superficialis of the fifth nerve
t trabecula
v vomer



HIGGINS NASAL ORGAN IN AMPHIBIA PLATE VIII

PLATE IX

EXPLANATION OF PLATE

Fig. 64.—Transverse section through the planum basale of *Necturus maculatus* 30 mm. long.
Fig. 65.—Transverse section through the posterior part of the fenestrated process of *Necturus maculatus* 45 mm. long.
Fig. 66.—Transverse section through the planum verticale of the younger larva of *Epicrium glutinosum*.
Fig. 67.—Transverse section through the same region of a 90 mm. Epicrium.
Fig. 68.—Transverse section through the planum basale of the same animal.
Fig. 69.—Transverse section through the planum verticale of the older *Amphiuma means* larva
Fig. 70.—Transverse section anterior to the planum verticale of *Amphiuma means* 82 mm. long.
Fig. 71.—Transverse section through the planum basale of the same animal.
Fig. 72.—Transverse section through the anterior planum basale of a larva of *Pipa americana*.
Fig. 73.—Transverse section slightly posterior to the above.
Fig. 74.—Transverse section through planum verticale of *Pipa americana*.
Fig. 75.—Transverse section through the choanal region of *Pipa americana*.
Fig. 76.—Transverse section through the external naris of *Hyla pickeringii*.

al p	alary process
anc	alinasal cartilage
ce	columna ethmoidalis
ch	choana
ct	cornu trabeculae
e	ethmoid bone
en	external naris
eng	external nasal glands
fen nb	fenestra naso-basalis
fen pr	fenestrated process
fr	frontal
ig	intermaxillary gland
jo	organ of Jacobson
le	lamina externa
m	maxillary bone
n	nasal bone
no	nasal organ
oc	oblique cartilage
ol	olfactory lobe
on	olfactory nerve
ond	dorsal root of olfactory nerve
onv	ventral root of olfactory nerve
oo	optic organ
p	profundus branch of the fifth nerve
pb	planum basale
pf	prefrontal
pm	premaxillary
pp	pterygoid process
ps	parasphenoid
pt	planum tectale
pv	planum verticale
s	superficialis of the fifth nerve
spc	superior prenasal cartilage
v	vomer

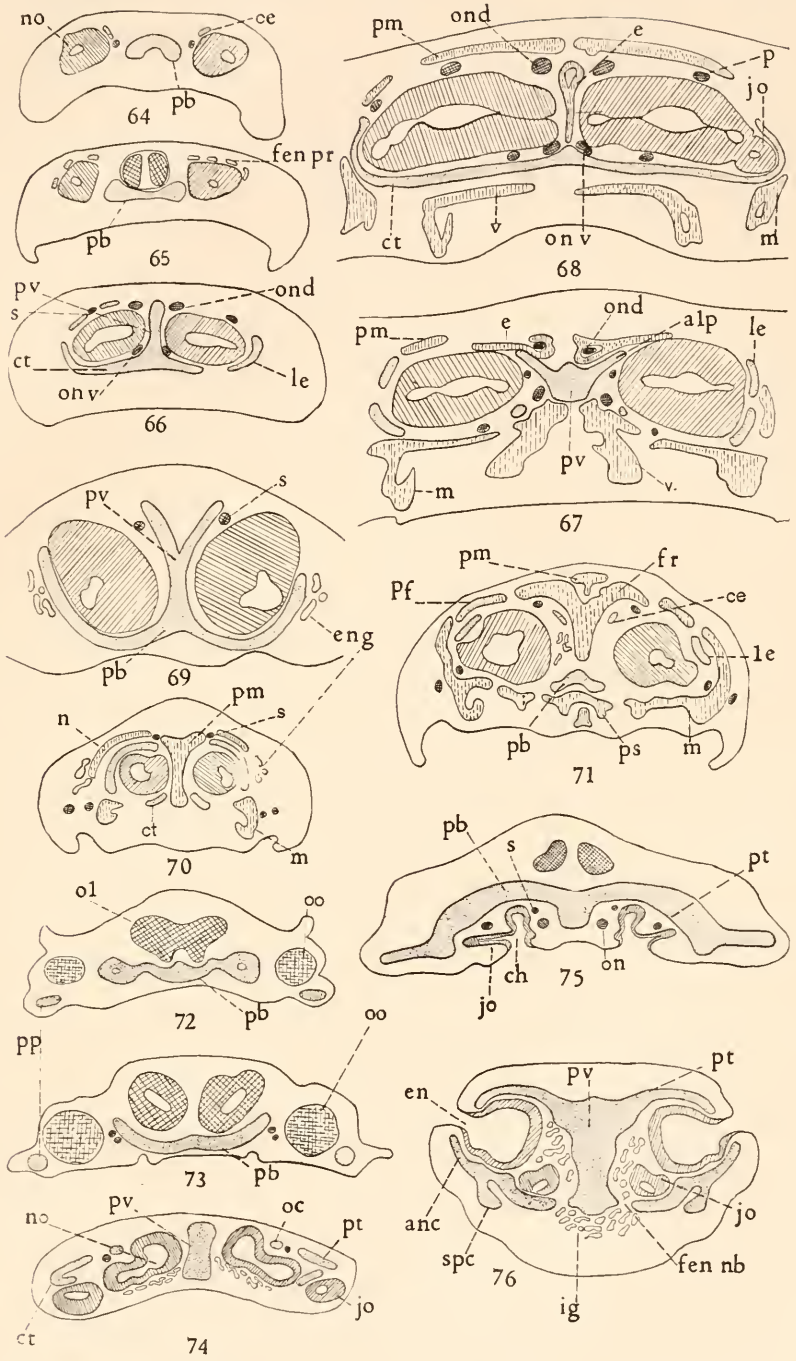
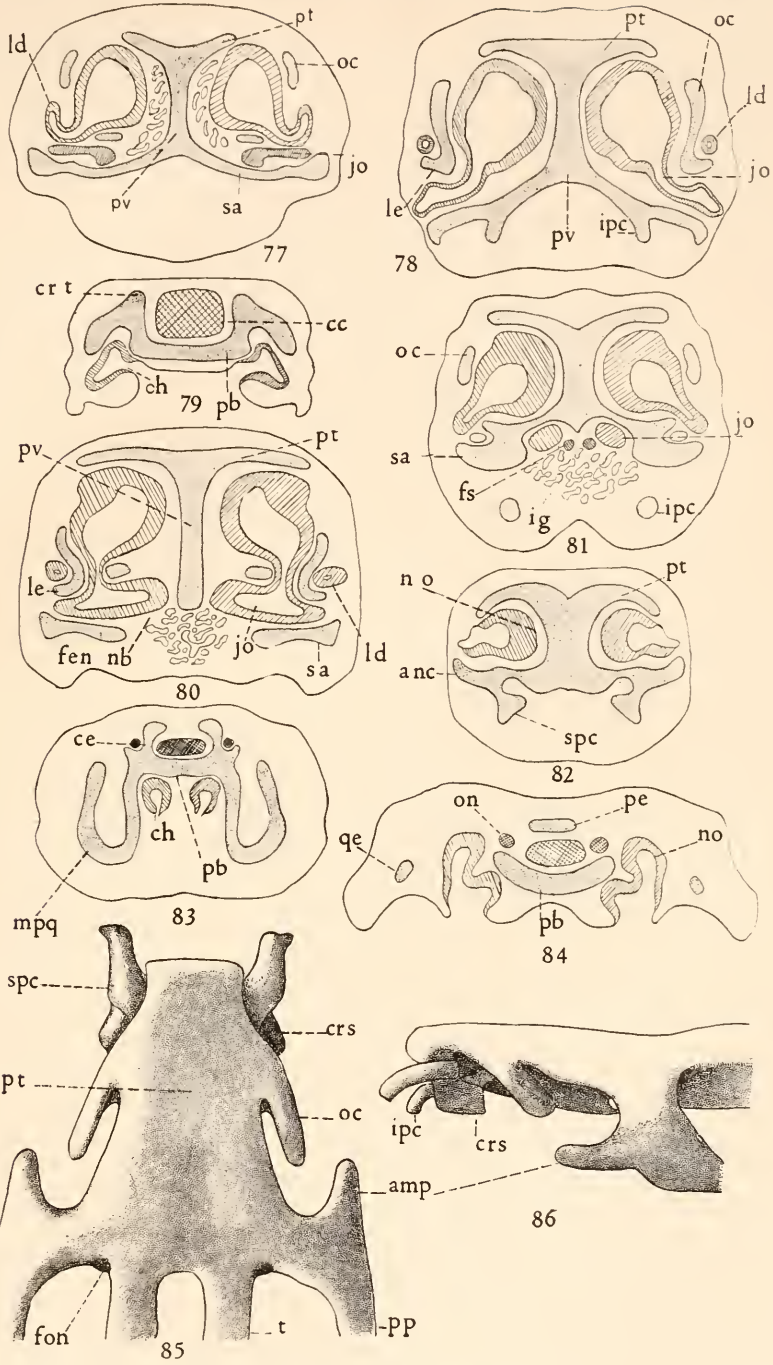

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74
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anc
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spc
76
fen nb
ig

PLATE X

EXPLANATION OF PLATE

Fig. 77.—Transverse section posterior to the external naris of the adult *Hyla pickeringii.*
Fig. 78.—Transverse section through the lamina externa of the same animal.
Fig. 79.—Transverse section through the choana of a 9 mm. *Bufo americana.*
Fig. 80.—Transverse section through the fenestra naso-basalis of Bufo.
Fig. 81.—Transverse section slightly anterior to the preceding section.
Fig. 82.—Transverse section through the external naris of the same animal.
Fig. 83.—Transverse section through the muscularis process of the quadrate of *Rana viridescens* 28 mm. long.
Fig. 84.—Transverse section through the pons ethmoidalis of the same animal.
Fig. 85.—Dorsal view of model of the nasal capsule of a young adult of *Rana viridescens.*
Fig. 86.—Side view of model of the nasal capsule of the same animal.

amp	anterior maxillary process	*le*	lamina externa
anc	alinasal cartilage	*mpq*	muscularis process of quadrate
cc	cavum cranii	*no*	nasal organ
ce	columna ethmoidalis	*oc*	oblique cartilage
ch	choana	*on*	olfactory nerve
cr s	crista subnasalis	*pb*	planum basale
cr t	crista trabeculae	*pe*	pons ethmoidalis
fen nb	fenestra naso-basalis	*pp*	pterygoid process
fon	foramen orbito-nasalis	*pt*	platum tectale
fs	frontal branch of superficialis	*pv*	planum verticale
ig	intermaxillary gland	*qe*	quadrato-ethmoidalis
ipc	inferior prenasal cartilage	*sa*	solum anterius
jo	organ of Jacobson	*spc*	superior prenasal cartilage
ld	lacrimal duct	*t*	trabecula


ld
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78
cr t
cc
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REVISION OF THE NORTH AMERICAN AND WEST INDIAN SPECIES OF CUSCUTA

WITH THIRTEEN PLATES

BY

TRUMAN GEORGE YUNCKER

THESIS

SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN BOTANY IN THE GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS

1919

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INTRODUCTION

It is now sixty years since the appearance of Engelmann's monograph of Cuscuta. This paper has served as the basis of our taxonomic knowledge of the dodders up to the present. Since Engelmann's time, however, great collections have been made in what was then practically unexplored territory and many new species have been found, a number of which have been described.

Inspection of the collections in different herbaria shows a great diversity of forms grouped under the same specific name, and the same form often classed under several different species. Also a great number of specimens show no attempt whatever at identification. This confusion is due, to a certain degree, to the fact that many of the distinguishing characters demand a microscopic examination before the species can be identified. This cannot be altered, and the botanist too busy to make dissections will probably never get beyond the guessing stage with many of the species. The different manuals and lists also show considerable confusion in the names applied to the different species and the range accredited to them. In attempting to make certain determinations it was frequently found that the plant in question could easily be called any one of two or three closely allied forms. Pictures had apparently never been made of many of the species.

It was with the hope of clearing up some of the confusion of nomenclature and descriptions and also to present the North American and West Indian species in such a manner that they could be recognized clearly that the present work was undertaken. The characters used in the keys have been taken, in so far as practicable, from the exterior of the flower and ordinarily evident under the hand lens. The keys, however, owing to the necessity of employing only floral characteristics, leave much to be desired.

Fifty-four species are treated in this paper, five of them are introduced, four from Europe and one from South America. Twenty-six species are found in the United States, seven of which are also reported from Canada; thirty-three in Mexico and seven in the West Indies. Of the West Indian species, with the exception of one that enters sparingly from Brazil, all are North American. Fourteen are found both in the United States and Mexico. Of the fifty-four species and forty-two varieties which are accounted for here fourteen species and sixteen varieties are described as new, and of the fifty-four species thirty-two are now figured for the first time.

ACKNOWLEDGMENTS

I am especially indebted to Professor William Trelease for his invaluable advice and criticisms throughout the course of the work. It was at his suggestion and under his supervision that the problem was worked out. During the process of the work collections of dodders in various herbaria have been studied. The collection at the Missouri Botanical Garden was opened to the writer and was of great value inasmuch as it contains Engelmann's herbarium, including his types, and allowed comparisons nowhere else possible. Besides this the collections studied are those of: University of Arizona, Boissier Herbarium, University of California, Connecticut Experiment Station, private herbarium of Mr. C. C. Deam, DePauw University, Gray Herbarium, University of Illinois, Michigan Agricultural College, New York Botanical Garden, United States National Museum, Wabash College, Rocky Mountain Herbarium in the University of Wyoming, and Yale University. At the Gray Herbarium and at the New York Botanical Garden, because of the limited amount of time at the writer's disposal, it was impossible to list all of the exsiccatae seen, though all specimens of Cuscuta were examined. The writer was granted the privilege of borrowing a large number of specimens from the latter herbarium, however, for more detailed study. To the gentlemen in charge of all these collections I tender my sincere thanks and appreciation of their courtesy in allowing me the privilege of studying these materials, without which the work could not have been done adequately. I also wish to thank Mr. F. H. Hillman of the United States Department of Agriculture for the abundant specimens and samples of seeds which he generously provided. Thanks are also due Professor W. Dudgeon of Allahabad, India, for four photographs showing tree-infesting dodders; as well as to numerous friends who have kindly sent me specimens.

HISTORY

Choisy was the first, in 1841, to treat Cuscuta monographically. Previous to this time little attention had been given the group. A few new species had been described from time to time from different parts of the world by travelers such as Humboldt and Gay. Choisy's paper, well illustrated, included all the species then known, forty-one, a large number being newly described by him. He considered the group as a genus belonging with the Convolvulaceae and used characters of the stigmas to divide it into two sections. The first section included those species possessing acute or clavate stigmas and the second those with globose-capitate stigmas. The second section in turn was divided into two subsections on the basis of the inclusion or exsertion of the styles, a character which is now considered of doubtful value inasmuch as the styles show different lengths depending upon the stage of development.

Shortly after the appearance of Choisy's paper Engelmann, in 1842, published his Monography of the North American Cuscutineae. He treated the group as a tribe of the Convolvulaceae, dividing it into two genera: (1) Cuscuta, with a gamosepalous 4–5 parted calyx and (2) Lepidanche, with 10–15 imbricated sepals. He described seven species of Cuscuta and one of Lepidanche, all of which he considered as new, but in a later paper he treated five of them as synonymous with previously described species.

In 1845 the ninth volume of de Candolle's Prodromus, in which the Convolvulaceae were treated by Choisy, made its appearance. Choisy here considered the dodders as a tribe of the Convolvulaceae and included forty-nine species. He included Engelmann's species, but considered most of them as doubtful or relegated them to synonymy.

Pfeiffer in the meantime had become interested in the dodders coming under his attention and, later in 1845, published a revision of the group. He did not believe it to be subordinate to but rather coordinate as a family with the Convolvulaceae and so treated it. He divided the family into three genera on the basis of stigmatic characters, as follows: (1) Cuscuta, with linear stigmas, (2) Epilinella, with clavate stigmas, and (3) Engelmannia with capitate stigmas. The following year (1846) he elaborated his original discussion and included Engelmann's genus Lepidanche.

Buchinger (1846) in reviewing Pfeiffer's article showed that his Engelmannia is untenable because of previous occupancy and suggested the substitution of Pfeifferia. This too, however, had been previously used to designate a genus of the Cactaceae. As early as 1790 Loureiro in his Flora Cochinchinensis had established a monotypic genus which he called Grammica. This genus was apparently unknown to Pfeiffer and Buchinger. Later the species included in this genus was shown to be a member of the group of Cuscutas possessing capitate stigmas. It would appear proper, therefore, to use the name Grammica to designate the members of any sub-group possessing similar characters, and Engelmann in a later paper uses it in this manner to designate those species with capitate stigmas.

Des Moulins published his Études organiques sur les cuscutes in 1853. He, like Pfeiffer, considered the group as an independent family and divided it into two tribes using the character of the circumscission of the capsule as a basis for the division. He showed that it is possible to further divide these tribes into five genera on the basis of the characters of the seeds, the capsules or the styles. He decided to use the styles as showing the best differential characters and proposed the following arrangement:

Capsule circumscissile. Tribe Cuscuteae

1. Styles filiform; seeds not winged.....Cuscuta

2. Styles clavate.....Epilinella
3. Style Single, capisate, ovoid.....Monogynella

Capsule not circumscissile. Tribe Cuscutinene

4. Styles capitase, globular.....Cassutha
5. Styles filiform; seeds winged.....Succuta

Des Moulins carefully considered the morphological details of the plants, but was at an apparent disadvantage on account of the limited number of species, about fifteen, known to him.

Engelmann, in 1859, after over twenty years of study in this country and abroad, published his Systematic Arrangement of the Species of the Genus Cuscuta. He considered the whole group as belonging to one genus of the Convolvulaceae which he divided into three sub-groups or sections. The first, comprising those species with linear stigmas and distinct styles, he called Cuscuta; the second, those species with distinct styles and capitate stigmas, Grammica, and the third, those with the styles more or less united and the stigmas of various shapes, Monogyna. These three groups he in turn divided into nine sections, including seventy-seven species, sixty-one varieties and four sub-varieties.

Engelmann had seen nearly all of the collections in the European and American herbaria and was able to relegate to synonymy a great many names that had been exercising botanists for many years. His ideas concerning the classification of these plants were well founded and,even in the light of present day knowledge, one finds it difficult to offer consistently any radical changes or improvements on his arrangement.

MATERIAL AND METHODS

The work, the results of which are recorded here, was carried on at the University of Illinois during the years 1917 to 1919 inclusive. Some time was spent in the libraries at Washington, D. C. and in studying the materials in different herbaria.

The studies were all made from dried herbarium specimens. It is possible that fresh specimens will show some variation from the descriptions given because of shrinkage and alterations attendant upon drying, but this can scarcely be avoided. The specimens were prepared for study in one of two ways. They were either soaked in a lacto-phenol solution[1] which is admirable for bringing the structures back to near their normal shape, or boiled in water. In either case the flowers were placed in water for study to prevent the collapsing of the parts. The objection to the use of the lacto-phenol solution is that it is necessary to leave the materials in it for some time (usually at least 48 hours) before they are soft enough to dissect. This is not the case, of course, with boiling when they can be

[1] Lacto-phenol stock solution: glycerine 40 parts; latic acid 20 parts; phenol crystals 20 parts; water 20 parts.

studied immediately. The corollas and calyces were split open and mounted on slides in glycerine jelly for study.

While the European species have been illustrated a number of times, our American forms in many instances have never been pictured. It is believed that the sketches illustrated in the plates will prove of value in making identifications. The types of most of the species treated have been studied and compared. All sketches were made with the aid of an Abbé camera lucida. The drawings were made from what were considered as normal specimens for the species and all details that would be considered as aids for identification are included. It should be remembered that the different species show a variation in their flowers that must be taken into consideration when making comparisons with the drawings. The flowers photographed were selected to show a normal form and possibly supplement the sketches somewhat. The plate illustrating the seeds of some of the different species allows a comparison of their relative shapes and sizes.

The original publication and the principal monographs treating each species have been cited. Because of the scarcity of good illustrations it was thought best to include citations of practically all known American illustrations.

MORPHOLOGY

Des Moulins in his Études was probably the first to use the characters of the seeds to differentiate groups of Cuscutas. He showed that it is possible to separate the genera on the differences in the shapes of their seeds. Different botanists have since studied the structure of the seed.

The number of seeds produced in each capsule varies from one to four, because of the abortion of one or more of the ovules. Certain species characteristically produce four seeds while others regularly produce but one or two. The shape of the seed is determined, to a certain degree, by the number developed in a capsule. When four are ripened they have two flattened surfaces and an outer convex surface. When but one is ripened, however, it generally possesses a spheroidal shape. The hilum is an oblong, linear or short, rounded, raised or sometimes sunken area situated towards one end or to the side of the seed. It is transverse, i.e. at right angles to the broadest diameter, or oblique. It is situated near the center of a roundish areola, the "umbilical area" of Engelmann and "seed scar" of Hillman (1907), which is usually smoother and of a different shade of color and may be somewhat striated. A cross section shows the seed to possess four layers of cells enclosing the spirally coiled, filamentous, acotyledonous embryo in the albumen. The outer layer of cells having their exposed walls somewhat convex and cuticularized gives a roughened appearance to the seeds. Guttenberg (1909) was able to show differences in the size and shape of the cells making up the testa and keyed out six species (*C. suaveolens*, *C. arvensis*, *C. epilinum*, *C. trifolii*, *C. europaea* and *C. arabica*).

The stems do not offer external characters sufficiently constant to aid in more than a general way in specific differentiation. Within certain limits the size is of use, but they show wide variation, even on the same plant. In describing the stems of the different species it has been thought best to divide them with relation to their diameters into three categories using comparative terms to designate each of them. Sections of an average stem were measured for each species, but sections from other parts of the same plant will show wide variation. The size varies from .10 mm. up to 1 or 2 mm. The term "slender" is used in the descriptions to designate those stems that ordinarily possess diameters of not more than .35 or .40 mm., the term "medium" for those of about .40 to .60 mm., and "coarse" for those with a diameter greater than .60 mm. Combinations of two of these terms as "slender to medium" are used in cases where the size of the stem lies about the border line between two of the divisions, as well as qualifying adjectives like "very slender." At the best, the size of the

stem is of small taxonomic value and undoubtedly varies with relation to the situation under which the parasite grows. It is a known fact that a plant of a certain species of dodder growing on an unfavorable host, as some grass for example, will not have the same luxuriance of growth and consequent large diameter of stem as another plant of the same species growing on a more favorable host like an Impatiens. The internodal length varies within wide limits and is probably determined to a great extent by environmental factors such as the food supply and the distance to be traversed before being able to fasten onto another stem.

The internal structure, however, according to Mirande (1900), exhibits characters which are of value. He was able to divide Cuscuta into three subdivisions by using characters of the vascular bundles. His histological division corresponds to that of Engelmann on external morphological characters. He finds that the Monogyna group shows bundle characters that, according to his opinion, are least modified by parasitism. The group Grammica, on the other hand, shows the greatest modification and reduction of parts, though Engelmann placed it intermediate, while the group Succuta, according to Mirande, holds an intermediate position. Further comparative study of the groups Succuta and Monogyna, which are predominatingly Old World species, may clear up the question regarding the sequence of forms.

The leaves of Cuscuta are reduced to scales which in themselves apparently offer no characters of taxonomic value. One usually subtends each branch and pedicel. They serve no apparent purpose, possessing but little if any chlorophyll and rarely functioning as photosynthetic organs. A few stomata are found on the scales of some species. Mirande has shown that the Monogyna group shows the least and the group Grammica the greatest amount of vascular reduction in the leaf.

It is in the flower that we find the effects of the parasitic mode of life least apparent and obtain the best characters for the separation of the different groups and the differentiation of species. The proportion of one part to another, their relative shape, size, and positions assumed offer fairly constant differential characters. Owing to the small size of the flowers some of the characters are difficult to determine without the aid of a magnifier. The size of the flower ranges from about 1 millimeter in length for *C. harperi* to 6 or 7 millimeters for the larger flowers, e. g. *C. rostrata*, *C. corymbosa*, etc. The size varies slightly for different individuals of a species. Identification of some species as *C. glomerata*, *C. compacta*, *C. ceratophora*, etc. can be made fairly accurately on external characters without dissection, but others like *C. californica*, *C. polygonorum*, etc. ordinarily require that a dissection be made to determine scale and staminal characters. The texture of the floral parts shows all

gradations from the more or less membranous to the thick, fleshy or even coriaceous types. In many species there are present in the calyx, corolla and capsular parts large pellucid or semi-pellucid glandular-appearing cells. The cells of the flowers in some species (*C. indecora* and *C. coryli*) are lens shaped giving the flowers a verrucose or papillate appearance and in others (*C. pentagona pubescens*, *C. gracillima saccharata*, etc.) these papillations are somewhat longer and give the flowers a pubescent appearance.

The calyx is gamosepalous in the majority of the species and always persistent. A small number, however, have the calyx segments entirely free. The shape, texture, degree of separation, and overlapping of the segments are characters that are useful for specific differentiation.

The corolla is always gamopetalous, and usually tubular or campanulate frequently becoming urceolate as the fruit matures. The length of the corolla lobes in comparison with the length of the tube; the shape of the tube and of the lobes; the position assumed by the lobes, that is, whether upright, spreading or reflexed; the texture of the corolla and the shape of the cells causing papillate forms, and the presence or absence of horn-like projections on the dorsal surface of the lobes are characters which aid in the separation of the species. In certain species the shape of the corolla is such that upon the maturation of the capsule the withered corolla is left at its base (*C. pentagona*); in others, because of its narrowness, it is torn loose from the base and carried either about the capsule (*C. californica*) or at its apex like a hood (*C. cephalanthi*).

Opposite the stamens and alternating with the lobes of the corolla are found a set of scale-like appendages in all but two of the North American species. The morphology and function of these organs are somewhat questionable. Babington (1844) thought that they were inserted opposite the corolla lobes and had become joined opposite the stamens. He considered also that, as they alternate with the stamens, they should be considered as an inner whorl of modified stamens.

Engelmann says (1859): "The most peculiar organs of the flower are the epistamineal scales, which are found in most of the species. The simplest form of that organ (in *C. inflexa*, *C. chlorocarpa*, etc.) exhibits a few teeth or lobes laterally adhering to the lower (attached) part of the filament. These lobes, in other species, expand into membranes, forming two lateral wings to the filament, crenulate or fringed at the tip and outside; then these wings partly united at their upper end, thus forming a single bifid scale; finally they unite entirely, forming an oblong, ovate, spatulate or truncate, more or less crenate or fimbriate scale. Towards the base the scales are always 'adnate in the middle,' or, properly speaking, attached to both sides of the adnate filament. Their bases usually connect with one another, forming inverted arches. . . . These scales are evidently

dilatations of the lower (attached) part of the filaments, perhaps of the character of stipules, as Prof. A. Braun suggests; or they are a sort of stamineal crown, attached at base to the corolla, but not a duplication of the same."

Miss Cunningham's idea regarding the origin of the scales does not agree with Engelmann's. She states (1898): "it was noticed that in some species the filament of the stamen extends under the apex of the scale, in others the base of the filament can be traced nearly to the base of the corolla, while the scale forms two lateral wings, one on either side of the filament. For this work specimens from each of the three groups were examined. Longitudinal sections were made through the corolla with its attached stamen and scale and a careful study showed that the scales have their origin from the corolla. The stamens also originate from the corolla, but at a different level from the scale so that they cannot possibly be attached to each other. However, in the third section a few species showed some connection between the scale and the filament; but, while there may have been a slight attachment of these parts in individual specimens, yet the examination of other sections fully demonstrated the fact that the origin of the scale is unquestionably from the corolla, and the base of the stamen is slightly above that of the scale. The results of these examinations, so far as made, confirm us in the belief that the scales are not epistamineal, and do not form a stamineal crown, but are petaloid and are in the nature of a duplication of the petals."

It would appear inconsistent with the morphology of a typical flower to consider the scales as outgrowths of the corolla and at the same time originating opposite the stamens. After examination of a great many specimens of different species and of sections made of many of them, it is quite evident to me that the scales are outgrowths of the filaments, as Engelmann believed. Inspection of various species in other genera of the Convolvulaceae shows that there are numerous filamentous appendages frequently present towards the base of the filaments. In *Convolvulus sepium*, for example, the filaments are found to be flattened laterally forming slight wings which bear numerous filamentous projections. It does not seem difficult to imagine these wings uniting at the base between two filaments forming the "inverted arch" or bridge, as I shall call this region and also uniting above and becoming free as the filament becomes more firmly attached to the corolla. I believe that the epistaminal scales of Cuscuta have originated in this manner. The scales are considered in the descriptions as continuing to the base of the corolla in all cases and the description of the height of the bridge is in relation to their total length. The bridge is of different heights and fairly characteristic for the different species. The shape, size and texture of the scales and the length and abundance of their processes is very different in

the various species. The different forms are fairly constant, and, within certain limits, offer good differential characters.

Their function is somewhat doubtful. Knuth says (1899): "In den weisslichen oder rötlichen, meist fünf-, aber auch vier-, drei- und zweizäligen Blüten wird der Honig durch fünf und weniger sich über dem Fruchtknoten zusammenbiegende Schuppen gegen Regen geschützt." Whether they serve any function other than this one of protection is rather doubtful.

The stamens are inserted at the top of the corolla tube. In some species (*C. exaltata*, *C. coryli*, etc.) the union of the filament to the tube below its separation is more or less evident, but in most of them it is not readily noticeable. The anthers range in shape from oblong-linear to orbicular, the shape being fairly characteristic for each species. They are introrse, adnate or more or less versatile, and open longitudinally. The pollen sacs are more or less divergent at their base in some species giving the anthers a sagittate appearance. In *C. polygonorum* and *C. glandulosa* the pollen sacs are frequently widely separated by a connective that reaches to the apex of the anther. This connective has been found somewhat prolonged into a slight apiculation in some specimens of *C. americana* and others. The filaments are slender or subulate, and somewhat oval in cross section. Their length shows a rather wide range. In some the anthers are quite sessile while in at least one species (*C. gracillima*) they are on filaments that are longer than the corolla lobes. This length of the filaments, however, is variable within certain limits for members of the same species.

The two-celled, four-ovuled ovary is ordinarily very small but even in the younger flowers gives an indication of the shape of the capsule-to-be. The ovules are basal, anatropous and provided with one integument. The styles are of different lengths and shapes for the different species. They are for the majority of the species as long as or longer than the ovary. In most of the species they are slender and of the same thickness throughout, but a number, chiefly Mexican, possess styles having a greater diameter at the base and tapering towards the stigma. The common position for the styles is upright, but in some species (*C. coryli*, *C. polygonorum*, *C. mitraeformis*, etc.) they become widely divergent as the fruit matures. In the group Monogyna the styles are united more or less completely; in the others they are entirely separated. The only representative of the Monogyna section found in this country so far is *C. exaltata*. Its styles, while more or less connate, are easily separable and show a distinct line of cleavage, indicating that the union is incomplete.

Two distinct types of stigmas are found. The North American forms all possess the semi-globular capitate type which characterizes the group Grammica, with the exception of *C. exaltata* which has the capitate type

but with the stigmas somewhat flattened. One or two species show stigmas somewhat irregular and convoluted. All of the species found so far in this country with the linear type of stigmas are Old World forms that are parasitic on economic plants. *C. europaea* has been found but three times in this country according to the records, and its apparent scarcity is probably because of the fact that it does not ordinarily parasitize crop plants and is unable to gain a foothold. The stigmatic characters are easily seen without dissections and are the most constant to be found in the flowers. These, with certain other characters, in correspondence with geographic distribution, seem to indicate the natural division of the group into its primary subdivisions.

The two carpels making up the capsule are not completely united in all the species. An opening extends down between the styles into the capsule in the most of them, but not, however, connecting with the interior of the cells. The size and depth of this opening, which Engelmann termed the "intrastylar aperture," is somewhat different for the various species.

The capsule may or may not be circumscissile, depending upon the species. The Old World forms, as well as most of those from Mexico and the southwestern part of the United States have capsules that open by a more or less regular line of cleavage towards the base. In some species a thickened ridge is formed which marks this line of separation. Most of the species, however, do not show this thickening, and, while the cleavage is ordinarily quite regular, in some species it is somewhat ragged. The partition wall composed of the adjacent walls of the two carpels up to the place where the intrastylar aperture begins is frequently left in the basal portion of the circumscissile capsule after opening. This is usually obcordate and is most admirably exhibited in *C. applanata* and *C. epilinum*. It may be somewhat difficult to predict the mode of dehiscence when examining young flowers, but with those with more mature capsules a slight pressure with the point of a pencil will usually cause the circumscissile type of capsule to break loose, while the non-circumscissile type will be crushed or will tear irregularly. In a careful dissection of young flowers of those species possessing a circumscissile type of capsule the ovary may often be detached if pulled, since the base ordinarily forecasts the line of circumscission of the mature capsule in having a weaker zone. The shape of the capsule is characteristic for the different species. It ranges from globose-depressed (*C. polygonorum*, *C. umbellata*, etc.) to globose-ovoid (*C. salina*, *C. denticulata*, etc.) or pointed (*C. gronovii*) or long-beaked, flask-shaped (*C. rostrata*). This variation in shape is due in some species to a thickening of the capsule wall at the apex (*C. gronovii*) but in others (*C. denticulata*) this is not true. Many species have the capsular wall thickened in the form of a ring or collar about the style bases and bordering the intrastylar aperture.

A number of variations from the normal type are found in this group. While the flowers, with but few exceptions, are typically pentamerous practically all species show flowers with but two, three or four parts. Pistils possessing three styles instead of two are rather common. In a number of specimens the stamens were found to be petaloid with abortive thecae, but in others the thecae were borne at the edge of the otherwise normal corolla lobes with no indication of filaments. In one flower of *C. pringlei* well developed scales were found on the exterior of the corolla; normal scales also being present. A few flowers of *C. ceratophora* exhibited unmistakable buds produced on the receptacle between the calyx and the corolla. Some species predominatingly produce their flowers endogenously, e.g. *C. glomerata*, as reported by Bessey (1884), Goebel (1908), Stevens (1889), Thompson (1899), etc. A number of other species have been seen in which endogenously formed flowers were found to be more or less frequently produced. In some specimens of *C. cephalanthi* practically all the flower clusters are so formed. When formed internally the flower clusters usually originate directly over haustorial areas and break forth in two more or less parallel rows.

Kuhn (1867) lists Cuscuta as one of a number of different "plantae floribus cleistogamis." Müller says (1883) of *C. epithymum* that it is homogamous and "honey is secreted by the lower part of the ovary and is sheltered by the scale-like appendages of the corolla. The flowers are visited by Sphegidae and in the absence of insects fertilize themselves." Knuth says (1899): "Die Staubfäden sind von Anfang an einwärts gekrumt, sie neigen sich später weiter nach innen, entweder bis zur Berührung mit der Narbe oder bis sie senkrecht über derselben stehen, so dass alsdann durch Pollenfall Bestäubung eintritt." and further: "Als Besucher bemerkte H. Müller 2 Grabwespen: *Crabo elongatulus*, einzeln, *Philanthus triangulum* mehrfach; Kohl in Tirol die Faltenwespe *Polistes gallica*."

Extended observations of a number of patches of dodder failed to reveal any insects alighting on the flowers. Mirande says (1900): "Le *Cuscuta fragrans* qu'on trouve aux environs d'Anthènes répand un agréable parfum de violettes; le *C. reflexa* de l'Inde, possède une odeur de fleurs d'oranger." A specimen of *C. racemosa chiliana* collected by Davis in California was recorded as "fragrant." It is probable that the plants exhibiting fragrance would be more liable to insect visits than those without it.

Cuscuta frequently is self parasitic, that is, often coiling about and sending haustoria into its own stems. Saccardo records *Dendryphium macowanianum* as parasitizing *C. cassythoides* and Peck records (1874) a new species of Protomyces (*P. martindalii*) as occurring on *C. gronovii*. A number of swollen stems and flower pedicels found during the course of

the study with cavities in them were indicative of galls caused by insects. It was not possible, however, to identify the insects causing the galls.

Engelmann makes the following statement (1843): "I am now convinced that although many Cuscutae prefer some plants to others, yet there is no constancy in this respect, but the same species often grows upon a great variety of widely different plants. I did wrong, therefore, to name them from the genera upon which they grew and I should much prefer to see the names of *C. cephalanthi* changed into *C. tenuiflora*, *C. coryli* into *C. incurva*, *C. saururi* into *C. umbrosa* Beyr.?, *C. polygonorum* into *C. chlorocarpa* and *Lepidanche compositarum* into *L. squarrosa* if they had not yet been published." Later he actually did make some of the substitutions mentioned. It is a fact that certain species apparently have a preference for certain host plants, but, as Engelman indicates, this is not a constant characteristic. Some species live predominantly, however, on certain classes of plants as, for example *C. exaltata* which is ordinarily found on trees, while *C. salina* shows a predilection for saline herbs, and so on. The majority prefer, however, the more succulent herbaceous plants.

Except for a few species parasitic on economic plants and liable to distribution by artificial means and a few species with a wide variety of forms they seem to be more or less limited in their distribution. There seem to have been originally two points of dispersal in North America. One was apparently somewhere in the eastern part of the United States, probably somewhere along the Appalachian range and the other in the southwestern part of the continent, either in Mexico or the southwestern United States. The species inhabiting the different regions possess group characteristics that are fairly typical of those regions. The species in the West Indies seem to be migrants from the United States and Mexico with the exception of *C. partita* which probably entered from Brazil; no species found in the islands so far is peculiar to them, but all are members of more or less predominant continental species.

Owing to the nature of their structure, fossil remains, so far as recorded, are lacking and an estimate as to the age of the plants in relation to the earth's history would be valueless.

SYSTEMATIC ARRANGEMENT OF THE GENUS

CUSCUTA (Tournefort) Linnaeus

Cuscuta Tournefort, Inst. Rei Herb., 1:652, t. 422, 1700.—Linnaeus, Spec. Pl., 124, 1753.—Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:268, 1841; and in DC., Prodromus, 9:452, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:453, 1859.—Bentham & Hooker, Gen. Pl., 2:881, 1873.—Peter, in Engler & Prantl, Die natürl. Pflanzenfam., Teil IV, Abteil. 3a, p. 37, 1897.

Epithymum (Plinius ex) Nieuwland & Lunell, Amer. Mid. Nat., 4: 511, 1916.

Hypogynous, sympetalous, herbaceous parasites. Stems filiform, twining about woody or herbaceous hosts from which they obtain their nourishment by means of haustoria. Leaves reduced to small functionless scales. Flowers small, more or less cymose clustered, mostly gamosepalous; usually pentamerous (infrequently tri- or tetramerous); stamens inserted in the throat, alternating with the corolla lobes; scale-like, more or less fringed or fimbriate structures present in most of the species at the base of the corolla opposite the stamens; ovary two-celled, each cell containing two anatropous ovules; styles distinct or united; stigmas capitate or linear-elongated. Fruit a capsule which remains closed or opens with a distinct line of circumscission near its base; embryo acotyledonous, filiform or with an enlargement at one end.

Key to the subgenera

Styles more or less united ..... MONOGYNA (p. 20).
Styles distinct.
Stigmas linear-elongated ..... SUCCUTA (p. 21).
Stigmas capitate ..... GRAMMICA (p. 25).

Sub-genus MONOGYNA Engelmann

Cuscuta group Monogyna Engelmann, Trans. Acad. Sci. St. Louis, 1:460, 1859.
Kadurias Rafinesque, Fl. Tellur., 4:91, 1836.
Aplostylis Rafinesque, Fl. Tellur., 4:91, 1836.

Stems very coarse. Flowers sessile or on short pedicels in spicate, racemose or paniculate cymes, pentamerous, the withered corolla remaining at the apex of the regularly circumscissile capsule or dropping off; styles thick, more or less completely united; stigmas capitate, subglobose to ovate or conic. Chiefly parasitic on woody hosts. Mostly Old World species, only one being found in North America.

Section MONOGYNELLA (Des Moulins) Engelmann

Cuscuta section Monogynella (Des Moulins) Engelmann, Trans. Acad. Sci. St. Louis, 1:512, 1859.

Monogynella Des Moulins, Études org. cusc., p. 65, 1853.

Flowers in spicate or racemose cymes; stigmas capitate, subglobose or ovate, on thick, more or less completely united styles; withered corolla always remaining at the apex of the capsule.

Cuscuta exaltata Engelmann

[Figures 6, 62 and 63]

C. exaltata Engelmann, Trans. Acad. Sci. St. Louis, 1:513, 1859.
C. gamostyla Engelmann, Trans. Acad. Sci. St. Louis, 1:513, 1859; in synon.

Stems thick and stout (1–2 mm.). Flowers glabrous, 4–5 mm. long, pentamerous, sessile or subsessile in spicate panicles; calyx lobes fleshy, thick, concave, ovate-orbicular, obtuse, overlapping, nearly or quite as long as the corolla tube, subtended by one or two smaller concave bracts; corolla tube cylindrical with only the lobes exserted; lobes ovate-orbicular, obtuse, overlapping; stamens included, sessile; anthers ovate; scales composed of two wings, one on either side of the filament attachment, bridged at about the middle, toothed along the upper portion, or in some specimens the two wings united and free forming the ordinary type of scale; ovary globose; styles equal, partially or completely united but separating easily when pulled; stigmas flattened. Capsule ovate-globose, circumscissile, 5–7 mm. long, carrying the withered corolla at the apex; seeds about 3–3.5 mm. long, somewhat rostrate and triangular; hilum oblong, oblique to transverse.

This species is the only one found so far in North America possessing united styles. It is commonly parasitic on trees, frequently on *Quercus*.

Type location: In Western Texas. Range: Texas and Florida.

Specimens examined: UNITED STATES: *Texas;* New Braunfels (Lindheimer 472, taken as type, in the Engelmann Herb.), on the Cibolo near San Antonio (Lindheimer in 1846), at the mouth of Pecos (Bigelow in 1851), Dallas Co. (Reverchon 663, 2552, in 1875 and in 1880), on the Blanco (Wright in 1847), Western Texas (Nealley 260), Bexar Co. (Jermy in 1904). *Florida;* Volusia Co. (Baker in 1918). This specimen, in the Gray Herbarium, so far as can be determined is identical with those collected in Texas.

Sub-genus SUCCUTA (Des Moulins) n. comb.

Succuta Des Moulins, Études org. cusc., p. 74, 1853, amplified.
Schrebera Linnaeus, Sp. Pl. (2 ed.), p. 1662, 1763.
Cassytha (Gesner. ex) S. F. Gray, Nat. Arr. Brit. Pl., 2:345, 1821.
Lepimes Rafinesque, Fl. Tellur., 4:91, 1836.
Cuscuta Pfeiffer, Bot. Ztg., 3:673, 1845.
Epilinella Pfeiffer, Bot. Ztg., 3:673, 1845.
Epithymum Opiz, Seznam, p. 40, 1852.
Cuscuta group Cuscuta Engelmann, Trans. Acad. Sci. St. Louis, 1:459, 1859.

Flowers sessile or pedicellate; styles equal, distinct; stigmas linear-elongated; capsule circumscissile or remaining closed. Natives of the Old World. Four species have been introduced into North America as parasites of cultivated crops.

Section EUCUSCUTA Engelmann

Cuscuta section Eucuscuta Engelmann, Trans. Acad. Sci. St. Louis, 1:460, 1859.

Styles as thick as or thicker than and slightly shorter than or exceeding the length of the elongated stigmas. Capsule circumscissile.

Key to the species

Styles, including the stigmas, exceeding the length of the ovary.
Calyx lobes triangular-ovate, acute, scarcely overlapping.....*C. epithymum* (p. 22).
Calyx lobes broadly ovate, somewhat fleshy pointed at the apex, overlapping.....
.....*C. planiflora* (p. 22).
Styles, including the stigmas, not exceeding the length of the ovary.
Flowers usually tetramerous, capsule pointed, calyx lobes not overlapping.....
.....*C. europaea* (p. 23).
Flowers usually pentamerous, capsule depressed, calyx lobes overlapping.. .....
.....*C. epilinum* (p. 24).

Cuscuta epithymum Murray
[Figures 2, 86 and 145]

C. epithymum Murray, Linn. Syst. (13 ed.), p. 140, 1774.—Engelmann, Trans. Acad. Sci. St. Louis, 1:461, 1859.—Hillman, Nev. Agr. Exp. Sta. Bull., No. 15, fig. 3, 1892.—Piper, Wash. Agr. Exp. Sta. Bull., No. 8, fig. 1, 1893.—Matthew, Bull. Torr. Bot. Club, 20, pl. 164, fig. 2, 1893.—Toumey, Ariz. Agr. Exp. Sta. Bull., No. 22, fig. 9, 1897.—Britton & Brown, Illustr. Flora, 3:27, fig. 2956, 1898; 2 ed., 3:49, fig. 3443, 1913.

Lepimes epithymum Rafinesque, Fl. Tellur., 4:91, 1836.

For European synonymy see Engelmann, Trans. Acad. Sci. St. Louis, 1:461, 1859.

Stems slender, sometimes reddish or purplish. Flowers about 3 mm. long, pentamerous, sessile and numerous in dense compact clusters; calyx as long as or shorter than the corolla tube, the lobes triangular, acute, sometimes purplish tipped; corolla campanulate; lobes triangular, acute, spreading, shorter than the tube; scales more or less spatulate, shorter than the tube, fringed about the upper part, bridged at about a third of their height; stamens shorter than the lobes; filaments longer than the oval anthers; ovary globose, with a slightly thickened apex; styles and stigmas about twice as long as the ovary; stigmas filiform, slightly longer than the style. Capsule globose, circumscissile, capped by the withered corolla; seeds about 1mm. long, rather rough, angled, compressed, ovate; usually four in a capsule; hilum short, oblong, transverse.

C. trifolii, which is ordinarily considered as a synonym of *C. epithymum*, is believed by Simkovics (Magyar Növénytani Lapok. Klausenburg, 2:145–153, 1878. Abs. in Just Bot. Jahresb., 6^1:332, 1880) to be a hybrid of *C. epithymum* and *C. europaea*.

Type locality: The prototype of Bauhin probably from Switzerland. Range: Throughout North America on leguminous hosts.

Specimens examined: UNITED STATES: *Massachusetts;* North Worcester (Lowe in 1916), Nantucket (Moore in 1918). *Connecticut;* Hartford (Bissell 1900, Parlin 875), Southington (Bissell 47, 78, 158). *Vermont;* Manchester (Day 409). *New York;* LeRoy (Hill 68–1909). *Pennsylvania;* Bethlehem (Bechdolt in 1889), Newcastle (Johnston in 1904). *Maryland;* Baltimore Co. (Schurtz in 1907). *Michigan;* Memphis (Ward), Shelby (Wear). *Missouri* (Martin in 1889), Cassidy (Davis 561). *Washington;* Seattle (Piper in 1898).

MEXICO: *Mexico* (Pringle 8514). *Coahuila;* Saltillo (Hitchcock in 1910).

Cuscuta planiflora Tenore
[Figures 4, 64 and 129]

C. planiflora Tenore, Fl. Nap., 3:250, 1824–1829.—Engelmann, Trans. Acad. Sci. St. Louis, 1:464, 1859.

C. gracilis Rydberg, Bull. Torr. Bot. Club, 28:501, 1901.
C. anthemi Nelson, Bot. Gaz., 37:277, 1904.

For the Old World synonymy see Engelmann, Trans. Acad. Sci. St. Louis, 1:464, 1859. Our form appears to be the same as *C. planiflora approximata* Engelmann, but in the absence of sufficient foreign materials for study this cannot be stated for a fact.

Stems slender. Flowers glabrous, about 2 mm. long, membranaceous or somewhat fleshy, white, sessile, in dense globular clusters; calyx lobes as long as the corolla, broadly ovate, overlapping, somewhat keeled, fleshy pointed at the apex; corolla tube cylindrical, becoming urceolate in fruit; lobes spreading, oval, obtuse to slightly acutish; scales ovate, about reaching the filaments, crenulate about the upper portion, bridged somewhat below the middle; stamens shorter than the lobes; filaments slightly subulate, as long as or longer than the oval, sagittate, versatile anthers; ovary globose; styles slightly subulate, equal, (including the stigmas) longer than the ovary; stigmas curving and reddish, about as long as the styles. Capsule globose, circumscissile, the withered corolla carried at the apex; seeds about 1 mm. long, light brown, finely punctated and more or less scurfy, usually four in a capsule, oval, or somewhat oblong, angled, rather robust; hilum short, oblong, transverse or oblique, sometimes scarcely visible.

Type locality: Probably near Naples, Italy. Type not seen. Range in North America: Throughout most of the western states from Washington and Wyoming south to Colorado and New Mexico, mainly on leguminous hosts.

Specimens examined: UNITED STATES: *Wyoming;* Between Sheridan and Buffalo (Tweedy 3492, the type of *C. gracilis*, in the N. Y. Bot. Gard. Herb.), Little Goose Fields (Willets 558), Laramie (Nelson 1139, 1210), Teton Forest Reserve (Brandegee in 1897), Wheatland (Fay in 1914), Seminole Mts. (Nelson 4936, the type of *C. anthemi*, in the Rky. Mt. Herb. Univ. Wyo.). *Utah;* Salt Lake City (Garrett 1002, Smith 1831), Ogden (Tracy & Evans in 1887), Provo (Tracy in 1887), Little Springs (Rydberg & Garrett 8541), without indication of locality (Hillman in 1899). *Nevada;* Reno (Heizer 345, Hillman), Ormsby Co. (Baker 1477), Nevada City (Hurst in 1890). *Colorado;* Fort Collins (without indication of collector 4222). *Washington;* Cascade Mts. (Kammerer 98). *Oregon;* Powder River Valley (Cusick 2341). *New Mexico;* San Juan Co. (Standley 8058). *California;* Siskiyou Co. (Brown 492), Yreka (Butler 536).

Cuscuta europaea Linnaeus
[Figures 5, 85 and 144]

C. europaea Linnaeus, Spec. Pl., p. 124, 1753.—Engelmann, Trans. Acad. Sci. St. Louis, 1:468, 1859.

No American synonymy. For the foreign synonymy see Engelmann, Trans. Acad. Sci. St. Louis, 1:468, 1859.

Stems medium to slender. Flowers about 2–3 mm. long on short, thick pedicels in globular, compact clusters, glabrous, mostly tetramerous, infrequently tri- or pentamerous; calyx lobes ovate, obtuse, shorter than

the corolla tube; corolla tube campanulate, becoming urceolate as the fruit develops; lobes upright to spreading, triangular, obtuse, overlapping; scales small, thin and difficult to make out, shorter than the tube, bifid and with few processes which are most prominent towards the apex, bridged at about a third of their height; stamens shorter than the lobes; filaments somewhat subulate, about equal to the oval or roundish, slightly versatile anthers; styles shorter than the globose, slightly pointed ovary; stigmas filiform, as long as or shorter than the styles, styles and stigmas together shorter than the ovary. Capsule globose-conic, capped by the withered corolla, circumscissile; seeds about 1.5 mm. long, usually four in a capsule, oval, compressed, slightly angled; hilum oblong, transverse.

Type location: The prototype of Bauhin probably from Switzerland. Casual in North America.

Specimens examined: UNITED STATES: *Maine;* Gilead (Furbish in 1897). *California;* near Clear Lake (Bolander 2673, in part).

WEST INDIES: *Haiti* (Poiteau).

Cuscuta epilinum Weihe
[Figures 3, 59 and 133]

C. epilinum Weihe, Archiv des Apothekervereins im Nördlichen Deutschland, 8:50–51,1824.—Choisy in DC., Prodromus, 9:452, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:470, 1859.—Matthew, Bull. Torr. Bot. Club, 20, pl. 164, fig. 1, 1893.—Britton & Brown, Illustr. Flora, 3:28, fig. 2957, 1898; 2 ed., 3:48, fig. 3442, 1913.

No American synonymy. For foreign synonymy see Engelmann, Trans. Acad. Sci. St. Louis, 1:470, 1859.

Stems slender to medium. Flowers about 3 mm. long, glabrous, sessile, in scattered compact glomerules; calyx as long as the corolla and somewhat loose about it; lobes broadly ovate, acute; corolla urceolate, early conforming to the shape of the capsule; lobes ovate-triangular, obtuse, shorter than the tube; scales shorter than the tube, spatulate-truncated, crenulate about the upper portion, thin, bridged somewhat below the middle; stamens shorter than the lobes; anthers ovate, subcordate, about as long as the somewhat subulate filaments; ovary depressed-globose; styles short, about equal to the linear, slightly tapering stigmas; the style and stigma together much shorter than the ovary. Capsule depressed globose, somewhat angled about the developing seeds, circumscissile, leaving the obcordate dissepiment in the calyx, carrying the withered corolla at the apex; seeds frequently occurring in pairs, about 1.2 mm. long, round or ovate to oval, angular, somewhat scurfy; hilum linear, oblong, transverse or oblique.

Type locality: Probably near Minden, in Western Germany. Range in North America: Eastern and central United States and in Canada, always, in the specimens examined, on Linum.

Specimens examined: A fragment of the type in the Engelmann herb. UNITED STATES: *Delaware;* Wilmington (Canby), Centreville (Tatnall in 1863, Commons in 1863), New Castle

Co. (Commons 5850). *New York;* Buffalo (Clinton), Albany (Beck), Kelloggsville (Kilborne in 1882), Greenwich (Schrenk in 1890). *Ohio;* New London (Dewey in 1902. *Michigan;* East Lansing (Wheeler in 1899). *Pennsylvania;* Lancaster Co. (Porter in 1863).

CANADA: (Pringle in 1880).

Sub-genus GRAMMICA (Loureiro) Engelmann

Cuscuta group Grammica (Loureiro) Engelmann, Trans. Acad. Sci. St. Louis, 1:459, 1859
Grammica Loureiro, Fl. Cochinch., 1:170, 1790
Kadula Rafinesque, Fl. Tellur., 4:90, 1836
Anthanema Rafinesque, Fl. Tellur., 4:90, 1836
Pentake Rafinesque, Fl. Tellur., 4:90, 1836
Nemepis Rafinesque, Fl. Tellur., 4:91, 1836
?Dastylepis Rafinesque, Fl. Tellur., 4:125, 1836
?Eronema Rafinesque, Fl. Tellur., 4:125, 1836
Lepidanche Engelmann, Amer. Journ. Sci. & Arts, 43:343, pl. 6, 1842
Engelmannia Pfeiffer, Bot. Ztg., 3:673, 1845; not Torrey & Gray, 1841 nor Klotzsch, 1841
Pfeifferia Buchinger, Ann. sci. nat., III, 5:88, 1846; not Salm-Dyck, 1845
Cuscutina Pfeiffer, Bot. Ztg., 4:492, 1846
Buchingera F. Schultz, Jahrb. f. Pharmacie, 1847; (cf. Bot. Ztg., 6:760, 1848)
Cassutha Des Moulins, Études org. cusc., p. 77, 1853

Flowers sessile or pedicellate; styles usually unequal, distinct; stigmas capitate; capsule circumscissile or remaining closed. All of the species found native in North America belong here. A small number parasitize economically important plants.

Key to the sections

Capsule circumscissile.....EUGRAMMICA (p. 25).
Capsule remaining closed.....CLISTOGRAMMICA (p. 47).

Section EUGRAMMICA Engelmann

Cuscuta section Eugrammica Engelmann, Trans. Acad. Sci. St. Louis, 1:476, 1859.

Capsule more or less regularly circumscissile. Flowers with or without numerous subtending bracts; a few species with distinct prongs on the dorsal surface of the corolla lobes; styles slender or tapering from broad bases. Typically of the southwestern and southern United States and of Mexico: a small number getting over into the West Indies.

Key to the subsections

Styles subulate, divisions of the flowers obtuse.
  Flowers not subtended by numerous bracts.....SUBULATAE (p. 25).
  Flowers subtended by numerous bracts.....LEPIDANCHOPSIS (p. 29).
Styles of about the same thickness throughout.
  Divisions of the perianth mostly obtuse.....OBTUSILOBAE (p. 30).
  Divisions of the perianth acute to acuminate.....LEPTILOBAE (p. 36).

Subsection SUBULATAE Engelmann

Cuscuta § Subulatae Engelmann, Trans. Acad. Sci. St. Louis, 1:476, 1859.

Flowers large; the perianth divisions mostly obtuse; styles subulate, stout, upright or mostly more or less divergent. Typically Mexican and West Indian species.

Key to the species

Calyx lobes orbicular or ovate, overlapping, without dorsal prongs (sometimes present in the first species).

Calyx lobes orbicular, denticulate; styles longer than the ovary and capsule, intrastylar aperture rather small.....*C. erosa* (p. 26).

Calyx lobes ovate, entire, styles shorter than the ovary and capsule.

Calyx lobes ovate, usually as long as broad, styles widely divergent; stigmas not particularly convoluted.

Corolla lobes about equalling the corolla tube; styles broadly conical .....*C. mitraeformis* (p. 26).

Corolla lobes usually shorter than the corolla tube; styles not so broadly conical.....*C. jalapensis* (p. 27).

Calyx lobes broader than long, styles not so widely divergent; stigmas rather larger and convoluted.....*C. rugosiceps* (p. 27).

Calyx lobes more elongated, each with a dorsal prong.

Corolla lobes oblong, obtuse; scales large, about reaching the filaments, bridged at about the middle.....*C. ceratophora* (p. 28).

Corolla lobes ovate, acutish; scales much reduced, shorter than the tube, scarcely bridged.....*C. chapalana* (p. 28).

Cuscuta erosa n. sp.

[Figures 8 and 61]

Stems medium. Flowers glabrous, about 3 mm. long, pentamerous, on pedicels as long as or longer than the flowers, closely clustered about the host in cymose panicles, somewhat reddish brown; calyx lobes orbicular, obtuse, denticulate, overlapping, cupped, membranous at the edges, fleshier in the median portion, sometimes with a short dorsal projection, nearly distinct, shorter than or equalling the corolla tube; corolla campanulate; lobes upright or spreading, about as long as or slightly shorter than the tube, oblong, obtuse, some flowers possessing more or less of a horn-like projection at the end of a thickened vein-like elevation on the dorsal surface of each lobe near the apex; scales broad, fringed, shorter than the tube, bridged at about their middle; stamens shorter than the lobes; anthers oval, about equal to the subulate filaments; styles subulate, longer than the globose ovary. Capsule globose, circumscissile, usually one seeded; styles stouter and more divergent, the withered corolla about the capsule or capping it; seeds about 1.5 mm. long, globose, ovate, compressed, with a short, linear, transverse line or a dot for a hilum.

Type locality: Sonora, Mexico. Range: Arizona and northern Mexico.

Specimens examined: MEXICO: *Sonora;* (Palmer in 1869, the type, in the U. S. Nat. Herb. as sheet 49,836).

UNITED STATES: *Arizona;* Santa Rita Mts., south of Tucson (Engelmann in 1880, Thornber 7219, 7220).

Cuscuta mitraeformis Engelmann

[Figures 27, 71, 141 and 154]

C. mitraeformis Engelmann in Hemsley, Diag. Pl. Nov., p. 54, 1880.

Stems coarse. Flowers glabrous, 4–6 mm. long, pentamerous, on short pedicels in compact globular clusters; calyx lobes about as long as the corolla tube, ovate, obtuse, unequal, overlapping, the larger lobes usually strongly and unevenly carinate, the others less so; corolla campanulate; lobes ovate, obtuse, about as long as the tube, spreading to reflexed; scales oblong, sometimes somewhat truncated, as long as the tube, deeply fringed; stamens shorter than the lobes; filaments subulate, equal to the oblong anthers; ovary conical; styles shorter than the ovary, subulate, continuing the outlines of the ovary; stigmas capitate, sometimes slightly convoluted. Capsule 5–8 mm. long, circumscissile, with the withered corolla about it; styles widely divergent like horns; seeds oval, about 2 mm. long, angled; hilum short, oblong, transverse.

Type locality: "Enroute San Luis Potosi to Tampico, Mexico." Range: Central and southern Mexico.

Specimens examined: MEXICO: Between San Luis Potosi and Tampico (Palmer Dec. 1878 to Feb. 1879, the type, in the Engelmann Herb.). *Vera Cruz;* Jalapa (Rose & Hay 6170), Orizaba (Smith 204). *San Luis Potosi;* Alvarez (Palmer 137). *Michoacan* (Pringle 4330).

Cuscuta jalapensis Schlechtendal

[Figures 26, 65 and 66]

C. jalapensis Schlechtendal, Linnaea, 8:515, 1833.—Engelmann, Trans. Acad. Sci. St. Louis, 1:478, 1859.

Stems medium. Flowers 3–3.5 mm. long, glabrous, pentamerous, in dense clusters, on pedicels as long as or shorter than the flowers; calyx shorter than the campanulate corolla, lobes overlapping, ovate, obtuse, somewhat thickened and verrucose along the middle; corolla lobes ovate, obtuse, shorter than the tube, upright to reflexed; scales about as long as the tube, fringed; stamens shorter than the lobes; anthers ovate, about equalling the slightly subulate filaments; ovary globose-conic, styles shorter than the ovary, strongly subulate. Capsule circumscissile, globose, surrounded by the withered corolla, the conical styles widely divergent; seeds about 1.5 mm. long, ovate; hilum narrow, transverse.

This species is closely allied with *C. mitraeformis* but seems to differ from it in the smaller flowers, more globose ovary and less conical styles.

Type locality: "Prope Jalapam Mexico." Range: Mexico.

Specimens examined: MEXICO: (Müller in 1853), Jalapa (Schiede 152, the type number, in the Engelmann Herb.), Mexico City (Bustamente 83), near Mexico (Graham 250). *San Luis Potosi;* San Luis Potosi (Palmer 631). *Chihuahua;* Chihuahua (Townsend & Barber 294, Pringle 291), Sierra Madre (Pringle 1342).

Cuscuta rugosiceps n. sp.

[Figures 1, 70 and 155]

Stems coarse. Flowers glabrous, 4–6 mm. long, sessile, in compact clusters; calyx large, campanulate, nearly as long as the corolla tube; lobes short, broad, unequal, obtuse, somewhat lobed at the sinuses, overlapping, frequently carinate; corolla campanulate; lobes ovate, obtuse,

spreading, shorter than the tube; scales reaching the filaments, fringed, bridged at about the middle; stamens shorter than the lobes; anthers oval, about equal to the somewhat subulate filaments; ovary small, somewhat conic, tapering into the subulate styles; stigmas large and more or less convoluted. Capsule circumscissile, with a very thick apex giving the capsule a conic appearance, surrounded by the withered corolla; seeds usually four in a capsule, round, compressed, about 1.4 mm. long; hilum at one end, short, elliptical or a dot; umbilical area somewhat finely striated.

This species resembles *C. jalapensis* somewhat in the shape of its capsule, but is different in the shape of its calyx and the short, broad lobes; from *C. floribunda* and *C. macrocephala* it differs in the short, subulate styles and the thickened apex of the capsule.

Type locality: State of Oaxaca, Mexico. Range: Western and southern Mexico.

Specimens examined: MEXICO: *Oaxaca;* Sierra de San Felipe (Pringle 4967, the type in the U. S. Nat. Herb. as sheet 252,219). *Jalisco;* Volcano of Colima (M. E. 347).

Cuscuta ceratophora, n. sp.

[Figures 29 and 72]

Stems slender. Flowers glabrous, about 3 mm. long, pentamerous, sessile, in compact clusters; calyx lobes slightly longer than the corolla tube or about equalling it, oblong, obtuse, with uneven edges and a mucronate tip, or the apex more obtuse with a horn-like projection from its dorsal surface near the tip; corolla lobes about as long as the campanulate tube, upright to spreading, oblong, obtuse, irregularly toothed at the apex and with a subapical horn-like projection; stamens shorter than the corolla lobes; anthers small, cordate, slightly versatile and shorter than the somewhat subulate and rather stout filaments; scales reaching the filaments, broad, ovate, fringed with short processes, bridged at about their middle; styles stout, much longer than the small, globose ovary; stigmas capitate. Capsule globose, circumscissile with a small opening; styles subulate and somewhat divergent; seeds not seen.

The collections of this species are all rather fragmentary, but it appears to be well characterized. In a number of flowers well developed buds were found between the calyx and corolla. This has not been observed, so far as recorded, in any other species.

Type locality: "États de Michoacan et de Guerrero," Mexico. Range: Southern Mexico and the lesser Antilles.

Specimens examined: MEXICO: "States of *Michoacan* and *Guerrero*" (Langlassé 438, the type, in the U. S. Nat. Herb. as sheet 385,946). *Vera Cruz* (Müller in 1853).

WEST INDIES: *Curaçao;* Patrick (Britton & Shafer 3069).

Cuscuta chapalana n. sp.

[Figures 11 and 69]

Stems medium. Flowers 3–4 mm. long, glabrous, pentamerous, subsessile, the pedicels much shorter than the flowers, in compact cymose

clusters; calyx deeply divided, shorter than or equalling the corolla tube; lobes ovate, acutish, thickened along the mid-portion of the dorsal surface which bears a short projection near the apex; corolla cylindrical, slightly baggy in the basal region; lobes shorter than the tube, somewhat overlapping, erect to spreading, ovate, acutish, with a prong-like dorsal projection near the apex; scales very small, reaching not more than the middle of the tube, oblong, with a few short processes at the truncated apex, scarcely bridged; stamens shorter than the lobes; filaments shorter than the somewhat oval, subsessile anthers; styles subulate, as long as or shorter than the small, globose-conic ovary; stigmas capitate. Not seen in fruit, but this quite evidently circumscissile.

This species resembles *C. corymbosa* somewhat but differs in its more deeply divided calyx and subulate styles.

Type locality: Near Lake Chapala, Jalisco, Mexico. Range: Known only from the type location.

Specimens examined: MEXICO: *Jalisco;* mountains near Lake Chapala (Pringle 5349, the type, in the U. S. Nat. Herb. as sheet 305,846).

Subsection LEPIDANCHOPSIS n. subsect.

Flowers sessile in compact more or less continuous clusters, subtended by numerous bracts; calyx lobes nearly distinct, obtuse.

Only one species has been found so far in this section. Some specimens are quite similar in habit to *C. glomerata.*

Cuscuta pringlei n. sp.
[Figures 13, 119 and 152]

Stems medium. Flowers glabrous, subsessile to sessile, about 4 mm. long, pentamerous, compacted into dense elongated clusters about the host plant much as in *C. glomerata* or more loosely paniculate; flower parts somewhat fleshy; calyx segments slightly united, ovate, cupped, appressed to the corolla, overlapping, subtended by several unequal bracts of much the same shape as the calyx lobes; edges of the bracts and calyx lobes slightly irregular and the thickened median portion reddish; corolla campanulate, lobes, oblong-ovate, spreading, about as long as the tube and with the edges slightly uneven; scales ovate, reaching the filaments, copiously fringed with medium length processes, bridged at or slightly above the middle; stamens shorter than the lobes; anthers oblong, about as long as the filaments; ovary globose-conic, becoming umbonate; styles longer than the ovary, exserted in fruit. Capsule umbonate, thickened at the apex, circumscissile with a slightly jagged edge leaving the obcordate dissepiment in the persistent calyx; seeds usually three or four in a capsule, about 1.5mm. long, angled, oval or roundish, light brown or chocolate brown, mottled?; hilum short, oblong, oblique to transverse or reduced to a roundish dot.

This is the only species seen possessing the combination of circumscissile capsule and numerous subtending bracts.

Type locality: Hillside near Guadalajara, Jalisco, Mexico.

Specimens examined: MEXICO: *Jalisco;* hillside near Guadalajara (Pringle 2472, the type, in the U. S. Nat. Herb. as sheet 49,852), *Vera Cruz;* Zacuapan (?) (Purpus 8175).

Subsection OBTUSILOBAE Engelmann

Cuscuta § Obtusilobae Engelmann, Trans. Acad. Sci. St. Louis, 1: 479, 1859.

Flowers mostly relatively large; calyx rather deep; lobes obtuse, more or less overlapping; styles slender. Typically of Mexico, the West Indies and the southern United States.

Key to the species

Flowers short, the corolla lobes about equalling the tube.
- Calyx lobes deltoid, slightly, if at all, overlapping ..... *C. applanata* (p. 30).
- Calyx lobes orbicular or ovate, overlapping ..... *C. tinctoria* (p. 31).

Flowers relatively long; corolla lobes shorter than the tube.
- Calyx deeply divided; lobes orbicular ..... *C. floribunda* (p. 32).
- Calyx cup deep; lobes short, broadly ovate.
  - Flowers about 3 mm. long; scales about reaching the filaments, bridged at the middle or above ..... *C. americana* (p. 32).
  - Flowers about 5–6 mm. long; scales shorter than the tube, bridged below the middle.
    - Corolla bulging outward between the furrowed stamen attachments; scales sparingly fringed; calyx lobes not greatly overlapping ..... *C. corymbosa grandiflora* (p. 35).
    - Corolla cylindrical, not particularly furrowed; calyx about reaching the middle of the corolla tube or shorter, lobes not greatly overlapping ..... *C. corymbosa stylosa* (p. 35)
    - Corolla cylindrical, not furrowed, scales prominent; calyx lobes broad, overlapping and somewhat angled at the sinuses; stigmas relatively large ..... *C. macrocephala* (p. 36).

Cuscuta applanata Engelmann

[Figures 30, 68 and 132]

C. applanata Engelmann, Trans. Acad. Sci. St. Louis, 1:479, 1859.
C. alata Brandegee, Univ. Calif. Publ. Bot., 3:338, 1909.

Stems medium to coarse. Flowers glabrous, pentamerous, 2–3 mm. long, somewhat fleshy or membranous, subsessile on pedicels shorter than the flowers, in dense cymose panicles; calyx slightly shorter than or equalling the corolla tube; lobes broad, triangular-ovate, obtuse, frequently irregularly keeled in the median portion and below the sinuses down onto the short pedicels; corolla campanulate, conforming in shape to the maturing capsule; lobes ovate to oblong, obtuse to acutish, with slightly uneven edges, spreading, nearly as long as or equalling the tube; scales longer than the tube, spatulate, fringed towards the apex with medium length processes, bridged at from one-quarter to one-third their height; stamens shorter than the lobes; anthers ovate, slightly cordate, about equal to the filaments; styles exserted, unequal, as long as or longer than the globose ovary; stigmas capitate. Capsule depressed-globose, some-

what four-sided about the developing seeds, circumscissile, leaving the obcordate dissepiment in the calyx, surrounded by the withered corolla; seeds brown, about 1.4 mm. long, oval, usually four in each capsule; hilum short, oblong, transverse to oblique.

This species somewhat resembles *C. pentagona* but is easily distinguished from it by the circumscission of its capsule. The type of Brandegee's *C. alata* is a small, strongly keeled form. Some of the smaller forms of *C. applanata* approach the larger forms of *C. potosina* but are differentiated from them by the possession of longer styles and more oblong, obtuse corolla lobes.

Type locality: "In Arizona Territory south of the Gila River." Range: Mexico, Texas, Arizona and New Mexico.

Specimens examined: MEXICO: *San Luis Potosi* (Palmer 631½), San Luis Potosi to San Antonio, Texas (Parry 500). *Puebla;* Puebla (Purpus 5730), Tehuacan (Rose & Rose 11413, Rose, Painter & Rose 9887, 9888, 10275, Rose & Hay 5866). *Durango* (Palmer 641), Mapimi (Palmer 517). *Chihuahua* (Pringle 784, Palmer 142 and 227), *Zacatecas;* San Juan Capistrano (Rose 2445). *Sinaloa;* Culiacan (Brandegee in 1904, the type of *C. alata*, in the Univ. Calif. Herb.).

UNITED STATES: *Arizona* (Wright 1623–541, Mexican Boundary Survey, taken as the type, in the Engelmann Herb.), San Francisco Mts. Forest Reserve (Leiberg 5965). *New Mexico* (Wright 1625), Rita de las Frijoles (Cockerell 20). *Texas;* Presidio (Trelease 342), El Paso (Stearns 205).

Cuscuta tinctoria Martius

C. tinctoria Martius in Engelmann, Trans. Acad. Sci. St. Louis, 1:480, 1859.—Progel in Martius, Flora Brasiliensis, 7: 379, pl. 126, fig. 6, 1871.

Stems medium to slender or in some specimens rather coarse. Flowers glabrous, 4–5 mm. long, pentamerous, sessile or subsessile, sometimes subtended by an ovate-orbicular, cupped bract, single or in dense glomerules of many flowers; calyx lobes unequal, orbicular or ovate, obtuse, overlapping, about as long as the corolla, sometimes keeled; corolla campanulate, becoming urceolate in fruit, thinner towards the base; lobes ovate, or somewhat oblong, obtuse, overlapping, upright or mostly spreading; scales reaching the filaments, bridged at about the middle or below; stamens shorter than the lobes; filaments about equal to the oval-oblong, somewhat versatile anthers; styles shorter or longer than the globose ovary, becoming exserted in fruit. Capsule depressed-globose or infrequently somewhat ovate and slightly pointed, circumscissile; seeds about 1.5 mm. long, three or four usually in each capsule, angled, olive brown; hilum oblong, linear, transverse, areola dark colored.

Cuscuta tinctoria typica

[Figures 16 a–e and 79]

Scales abundantly fringed, bridged at about the middle; styles as long as or usually exceeding the ovary and capsule.

Type locality: Oaxaca, Mexico. Range: Throughout Mexico and to Guatemala.

Specimens examined: Mexico: *Oaxaca;* Oaxaca (Karwinski in 1827, taken as the type, a specimen in the Engelmann Herb.), Between Victoria and Rio Blanco (Karwinski in 1842). *Jalisco* (Pringle 4529, Palmer 579, Rose & Painter 7473). *Puebla;* Tehuacan (Purpus 5708), Puebla (Purpus 3553). *Coahuila & Neuvo Leon* (Palmer 918). *San Luis Potosi;* San Luis Potosi (Parry & Palmer 631, Palmer 87, Schaffner 377, 781, labelled *C. zacatlasculi* n. sp., Gregg 570). *Querctaro;* Queretaro (Rose & Rose 11150).

Guatemala: (Heyde 287), Quiché (Heyde & Lux 2912), Totonicapam (?Lehmann 1682).

Cuscuta tinctoria kellermaniana n. var.

[Figure 16 f–g]

Scales oblong, quite sparingly fringed, bridged at about a third of their height; styles shorter than the globose-depressed ovary and capsule.

Type locality: Volcano Agua, Guatemala.

Specimens examined: Guatemala: Volcano Agua (Kellerman 7567, the type, in the New York Bot. Gard. Herb.).

Cuscuta floribunda Humboldt, Bonpland & Kunth

[Figure 10]

C. floribunda Humboldt, Bonpland & Kunth, Nov. Gen. et Sp., 3:96, 1818.—Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:283, 1841; and in DC., Prodromus, 9:459, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:481, 1859.

Flowers about 4 mm. long; calyx lobes orbicular, obtuse, overlapping, shorter than the corolla tube; corolla cylindrical; lobes ovate-oblong, obtuse, between one-half and three-quarters as long as the tube, reflexed; scales somewhat triangular, reaching the filaments, rather sparingly fringed with medium length processes; filaments subulate; anthers ovate. Capsule globose with a thickened apex and ridge or collar about the intrastylar aperture; styles longer than the capsule. Seeds not seen.

The fragment of the type from which this description is drawn is in the Engelmann herbarium. It apparently possesses characters that distinguish it from all others.

Type locality: "in calidis Novae Hispaniae, prope pontem Istlae."

Specimens examined: At the Bridge of Istla, western Mexico (Bonpland, the type, a fragment in the Engelmann Herb.).

Cuscuta americana Linnaeus

C. americana Linnaeus, Spec. Pl., p. 124, 1753.—Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:282, pl. 4, fig. 4, 1841; and in DC., Prodromus, 9:459, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:482, 1859.—Progel in Martius, Flora Brasiliensis, 7:376, pl. 126, fig. 1, 1871.

Nemepis americana Rafinesque, Fl. Tellur., 4:91, 1836.

?Nemepis prolifera Rafinesque, Fl. Tellur., 4:91, 1836.

?Dastylepis brownei Rafinesque, Fl. Tellur., 4:125, 1836.

?Eronema robinsoni Rafinesque, Fl. Tellur., 4:125, 1836.

Stems medium to coarse. Flowers glabrous, 2.5–4 mm. long, pentamerous, subsessile in cymose, racemose, compact or somewhat loose clusters; calyx tubular, as long as or somewhat shorter than the corolla tube; lobes ovate-orbicular, overlapping, obtuse, short; corolla cylindrical, included

in the calyx with usually only the short, ovate, obtuse, upright to slightly spreading lobes exserted, but becoming exserted on the capsule; scales triangular, or sometimes somewhat oblong, fringed, shorter than the tube or sometimes reaching the base of the stamens, usually bridged about the middle or above; stamens subsessile, on filaments shorter than the anthers, included; anthers oval and in some specimens with the connective produced into a slight apiculation; styles longer than the globose ovary, becoming exserted, slender; stigmas capitate. Capsule globose-ovoid, circumscissile, capped by the withered corolla; seeds about 1.5 mm. long, light brown, usually but one or two in a capsule, ovoid, slightly compressed, with an indentation running lengthwise; hilum small, oval, oblique or reduced to a rounded spot.

It is rather questionable what species of Cuscuta Linnaeus referred to as *C. americana*. It has been thought best to retain the name for this species, as indicated by Engelmann. For a discussion of the confusion regarding the name see Coulter (1904).

There appear to be two forms of this species based more or less on difference in size. One, variety *congesta*, is common in Mexico and the West Indies, while the other, variety *spectabilis*, is rather closely confined to the West Indies.

Cuscuta americana congesta Progel
[Figures 22, 109 and 138]

C. americana congesta Progel in Martius, Fl. Brasiliensis, 7:376, 1871.

C. congesta Bentham, Bot. Sulph., p. 138, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:482, 1859; in synon.

C. leiolepis Miquel, Linnaea, 18:247, 1844.—Engelmann, Trans. Acad. Sci. St. Louis, 1:482, 1859; in synon.

C. surinamensis Schilling, Comm. Lepra., p. 200, t. 2, 1778.—Engelmann, Trans. Acad. Sci. St. Louis, 1:482, 1859; in synon.

C. campanulata Nuttall in Engelmann, Trans. Acad. Sci. St. Louis, 1:482, 1859; in synon.

Flowers about 2–3 mm. long, closely compacted in many flowered clusters, usually dark brown in herbarium specimens; stamens frequently with an apiculation of the connective; capsule ovoid, usually one-seeded; scales ordinarily bridged above the center.

Type locality: Acapulco, Guerrero, Mexico. Range: Throughout the West Indies and in Mexico.

Specimens examined: Fragments of the types of *C. campanulata* and *C. leiolepis* in the Engelmann Herb. West Indies: *Bahamas;* Cat Island (Britton & Millspaugh 5925, 5963), Grand Turk Island (Millspaugh & Millspaugh 9029), Governor's Harbor (Hitchcock in 1890, Britton & Millsphaugh 5519), Berry Islands (Britton & Millspaugh 2208), Exuma Chain (Britton & Millspaugh 2811). *Cuba;* El Cobre (Britton, Cowell & Shafer 12887), Rio San Juan (Britton, Earle & Wilson 5917), Guantanamo Bay (Britton 1910), Santa Clara Prov. (Combs 546). *Isla of Pines* (Britton, Wilson & Selby 14493, Britton, Wilson & Leon 15321). *Santo Domingo* (Rose, Fitch & Russell 3691). *Haiti* (Nash & Taylor 1578), Les Cayes (Favrat 41). *Jamaica* (Britton 3897), Hope Road (Harris 6975), Kingston (Britton 3006,

Hitchcock in 1890). *St. Thomas* (Britton, Britton & Shafer 43). *Barbados* (Dash 628). *Guadeloupe* (Père Duss 2468). *Martinique* (Père Duss 1878, Sieber 91). *Grenada* (Broadway in 1905). *Curaçao* (Britton & Shafer 3065).

Mexico: *Sonora* (Hartman 236), Guaymas (Brandegee in 1893, Palmer 331). *Guerrero* (Langlassé 127), Acapulco (Bentham, the type of *C. congesta*, a fragment in the Engelmann Herb. taken as the type, Palmer 341). *Sinaloa;* Mazatlan (Gregg in 1849, Rose, Standley & Russell 13727, Brandegee in 1893). *Yucatan* (Linden).

Cuscuta americana spectabilis Progel

C. americana spectabilis Progel in Martius, Fl. Brasiliensis, 7:377, 1871.

C. spectabilis Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:283, pl. 5, fig. 1, 1841; and in DC., Prodromus, 9:459, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:483, 1859; in synon.

C. globulosa Bentham, Bot. Sulph., p. 138, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:483. 1859: in synon.

Flowers 3–4 mm. long, less densely compacted in fewer flowered clusters; flowers ordinarily of a lighter color and rather more membranous; stamens ordinarily not apiculate; scales somewhat more deeply bridged and fringed; capsule slightly depressed and ordinarily two-seeded with the seeds larger.

Type locality: "Hab. circa Bahiam." Type not seen. Range: In the West Indies throughout the Greater Antilles and the Leeward Islands and sparingly in Mexico.

Specimens examined: West Indies: *Bahamas;* Anguilla Islands (Wilson 7983). *Cuba* (Linden 1994, Wright 1659 in part & in 1865, Bro. Hioram 2279, Pollard & Palmer 393), Santiago (Hamilton 16). *Porto Rico* (Sintenis 3239, Britton, Britton & Marble 2227, Heller 1899, 6169, Goll 565, 711, Underwood & Griggs 636, Britton & Wheeler 224, Britton, Cowell & Britton 5379). *Virgin Gorda* (Britton & Fishlock 1101). *St. Thomas* (Kuntze 555, 556, Holton, Britton, Britton & Shafer 137). *Tortola* (Britton & Shafer 707, Fishlock 489) *Santo Domingo* (Poiteau in 1802, in 1845, Wright, Parry & Brummell 391, Fuertes 194). *Haiti* (Nash 759), Azua (Rose, Fitch & Russell 3853), Santo Domingo City (Rose, Fitch & Russell 3763). *St. Croix* (Ricksecker 93, 313, 313a, Rose, Fitch & Russell 3604, 3608). *Montserrat* (Shafer 31). *Antigua* (Rose, Fitch & Russell 3279).

Mexico: *Gucrrero;* Acapulco (Bentham, the type of *C. globulosa*, a fragment in the Engelmann Herb.). *Yucatan* (Gaumer 705, a more elongated form).

Cuscuta corymbosa Ruiz & Pavon

C. corymbosa Ruiz & Pavon, Fl. Peruv., 1:69, pl. 105, fig. b, 1798.—Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:276, 1841; and in DC., Prodromus, 9:456, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:483, 1859.

Kadula corymbosa Rafinesque, Fl. Tellur., 4:90, 1836.

Stems medium. Flowers glabrous, 4–7 mm. long, pentamerous, subsessile on pedicels much shorter than the flowers, forming a more or less corymbose-paniculate inflorescence; calyx membranous, loose about the corolla, angled, lobes short, broad, obtuse, slightly overlapping, scarcely reaching, or exceeding the middle of the corolla tube; corolla more or less globular and furrowed along the stamen attachments in the lower part, or cylindrical and scarcely furrowed; lobes about a fourth as long as the

tube, ovate, obtuse, upright to spreading; scales narrow, with rather short, scattered processes, shorter than the tube, adnate for the larger part of their length, bridged below the middle; stamens about half as long as the lobes; filaments shorter than the oval anthers; styles longer than the small, globose or ovoid ovary, becoming exserted. Capsule small, globose, circumscissile, somewhat glandular, capped and surrounded by the withered corolla; seeds about 1.5 mm. long, robust, compressed, one to four in a capsule, oblique; hilum short, oval, oblique or transverse.

Cuscuta corymbosa grandiflora Engelmann

[Figures 24 a–e and 104]

C. corymbosa grandiflora Engelmann, Trans. Acad. Sci. St. Louis, 1:483, 1859.—Progel in Martius, Fl. Brasiliensis, 7:377, pl. 126, fig. 2, 1871.

C. popayanensis Humboldt, Bonpland & Kunth, Nov. Gen. Sp. Pl., 3:123, 1818.—Choisy in DC., Prodromus, 9:460, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:483, 1859; in synon.

C. cymosa Willdenow in Roemer & Schultes, Syst., 6:205, 1820.—Engelmann, Trans. Acad. Sci. St. Louis, 1:483, 1859; in synon.

C. inclusa Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:275, pl. 2, fig. 2, 1841; and in DC., Prodromus, 9:455, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:483, 1859; in synon.

C. patens Bentham, Bot. Voy. Sulph., p. 35, 1844.—Engelmann, Trans. Acad. Sci. St. Louis, 1:483, 1859; in synon.

C. laxiflora Bentham, Bot. Voy. Sulph., p. 138, 1845.—Engelmann, Trans. Acad. Sci.. St. Louis, 1:483, 1859; in synon.

Flowers large (5–7 mm. long); anthers nearly or quite sessile; corolla furrowed along the stamen attachment, particularly in the lower portion, bulging between the furrows; scales set out on more or less of a ridge away from the corolla in many specimens; capsule globose; calyx more than half as long as the tube.

Type locality: New Granada? Type not seen. Range: Central Mexico south to Guatemala and Costa Rica.

Specimens examined: Mexico: (Berlandier 1103, the type of *C. inclusa*, a specimen of the type number in the Engelmann Herb., Hahn 18). *Lower California;* Magdalena Bay (Bentham, the type of *C. patens*, a fragment of the type in the Engelmann Herb.). *Jalisco* (Pringle 4331). *Federal District;* Valley of Mexico (Pringle 11306 or 1130C). *Tepic;* Acaponeta (Rose, Standley & Russell 14329). *Tamaulipas;* Victoria (Palmer 56). *Guerrero;* Acapulco (Bentham, the type of *C. laxiflora*, a fragment of the type in the Engelmann Herb.).

Gautemala: Alta Vera Paz (von Türckheim II 1547), Mazatenango (Kellerman 4591, Bernoulli 59), San Felipe (Kellerman 5576), Acutima (Smith 1912), Solola (Kellerman 5916a).

Costa Rica: (Tonduz 11750).

Cuscuta corymbosa stylosa Engelmann

[Figures 24 f and 110]

C. corymbosa stylosa Engelmann, Trans. Acad. Sci. St. Louis, 1:484, 1859.

C. stylosa Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:283, pl. 5, fig. 2, 1841; and in DC., Prodromus, 9:459, 1845.

Flowers shorter than in the preceding variety (4–5 mm. long). Corolla cylindrical and slightly, or not at all ventricose; calyx not ordinarily

reaching beyond the middle of the tube; filaments sometimes as long as the anthers; ovary globose-ovoid to conic. Choisy's figure of the flowers of this variety does not correspond with the specimen of the type number examined, showing the division of the calyx too deep, etc.

Type locality: Mexico. Range: Central and southern Mexico.

Specimens examined: MEXICO: (Berlandier 822, the type of *C. stylosa*, a specimen of the type number in the Engelmann Herb.). *Federal District;* Valley of Mexico (Pringle 6574). *Puebla* (Nelson 2014). *Vera Cruz;* Vera Cruz (Parry & Palmer in 1877), Orizaba. (Müller 1260), Zacuapan (Purpus 5745, 7564, 7775). *Hidalgo;* Zimapan (Galeotti 1412). *Mexico;* Toluca (Andrieux 214), Guadaloupe, Vallé de Mexico (Bourgeau in 1866), Vallé de Cordova (Bourgeau in 1866). *Chiapas;* Comitan (Linden).

Cuscuta macrocephala Schaffner, n. sp.

[Figures 19 and 108]

C. macrocephala Wilh. Schaffner in herb.

Stems coarse. Flowers glabrous, 5–6 mm. long, pentamerous, on pedicels as long as or shorter than the flowers in scattered cymose clusters; calyx deep, texture thick and rather fleshy, nearly covering in most specimens the cylindrical corolla, somewhat angled below the sinuses; lobes short, broadly ovate, lobed, overlapping; corolla lobes short, broadly ovate, obtuse, overlapping, lobed, upright to slightly spreading; scales deltoid-oblong, shorter than the corolla tube, shallowly fringed, bridged at, or somewhat below, the middle; stamens sessile; anthers oval; styles much longer than the globose or slightly conic ovary; stigmas broad (about .8 mm.), globular or slightly conic. Capsule circumscissile, globose, the withered corolla carried at the apex; seeds about 2 mm. long, one to four in each capsule, oval, angled; hilum a narrow transverse line.

This species somewhat resembles *C. corymbosa grandiflora*, from which it differs in the corolla not bulging between the stamen attachments, in the somewhat cordate lobes and their greater overlapping, and in the more prominent scales and larger stigmas.

Type locality: Culiacan, Sinaloa, Mexico. Range: Central and northern Mexico.

Specimens examined: MEXICO: *Sinaloa;* Culiacan (Schaffner, without date or number, the type, in the N. Y. Bot. Gard. Herb., Brandegee in 1904). *Tamaulipas;* Victoria (Palmer 52). *Lower California;* San José del Cabo (Brandegee in 1897), San Bartolomé (Brandegee 409), Todos Santos (Brandegee in 1890), La Paz (Palmer 141).

Subsection LEPTILOBAE Engelmann

Cuscuta § Leptolobae Engelmann, Trans. Acad. Sci. St. Louis, 1:485, 1859.

Flowers mostly smaller; calyx lobes acute to acuminate; corolla lobes mostly as long as or longer than the tube—in the last three species somewhat shorter; styles slender, longer than the ovary. Chiefly of Mexico, the West Indies and the southern and western United States.

Key to the species

Calyx about equalling or exceeding the corolla (shorter in *C. deltoidea*).

Flowers ordinarily at least 2.5–3 mm. long; calyx lobes overlapping.

Anthers subsessile or sessile, flowers tetra- or pentamerous.....*C. purpusii* (p. 37).
Anthers on filaments about as long as or longer than the anthers.
Scales reaching the filaments, fringed, bridged at about the middle.
Corolla cylindrical, lobes lanceolate, acuminate, without a dorsal projection.....*C. choisiana* (p. 38).
Corolla campanulate, lobes ovate, obtusish, ordinarily with a dorsal projection.....*C. odontolepis fimbriata* (p.39).
Scales shorter than the tube, oblong, toothed about the apex, bridged below the middle.....*C. odontolepis* (p. 38).
Flowers mostly smaller; calyx lobes overlapping in one species, not overlapping in the others.
Styles not exceeding the ovary or capsule in length; scales rather sparingly fringed.....*C. potosina* (p. 39).
Styles longer than the ovary and capsule; scales ordinarily rather abundantly fringed, but reduced to wings in one variety.
Flowers reddish; corolla deeply furrowed along the stamen attachments.....*C. partita* (p. 40).
Flowers whitish; corolla not deeply furrowed.
Calyx segments not overlapping, as long as the corolla tube.
Calyx segments lanceolate, acuminate, scales shorter than the tube, fringed or reduced to wings.....*C. desmouliniana* (p. 40).
Calyx segments mostly triangular-acute to lanceolate; scales as long as or exceeding the tube (shorter in one variety of *C. umbellata* and reduced or absent in one variety of *C. gracillima*)
Corolla lobes entire.
Flowers 2–7 mm. long; stamens shorter than the lobes; scales bridged below the middle; flower clusters rather loose and diffuse; stems profuse....*C. umbellata* (p. 41).
Flowers about 2 mm. long; stamens longer or shorter than the lobes; scales bridged at about the middle or reduced in one variety; flower clusters globular; stems ordinarily disappearing from between the flower clusters.....*C. gracillima* (p. 43).
Corolla lobes deeply serrated or lacerated....*C. lacerata* (p. 44).
Calyx segments overlapping, shorter than the corolla tube.....*C. deltoidea* (p. 44).
Calyx much shorter than the elongated corolla.
Calyx lobes keeled or tuberculate, pentamerous.....*C. tuberculata* (p. 45).
Calyx lobes not keeled, penta- or tetramerous.
Flowers 3–4 mm. long, calyx papillate; corolla papillate in basal portion, scales bridged at about the middle or below.....*C. leptantha* (p. 45).
Flowers 4–5 mm. long; calyx and corolla glabrous; scales bridged at about a third of their height.....*C. polyanthemos* (p. 46).

Cuscuta purpusii n. sp.

[Figures 23 and 90]

Stems slender to medium. Flowers glabrous, pentamerous (infrequently tetra- or trimerous), about 4 mm. long, on pedicels as long as or longer than the flowers in loose, few-flowered, cymose panicles; calyx nearly as long as or longer than the corolla; lobes ovate-triangular, acute, somewhat lanceolate, slightly lobed at the base, overlapping, tips somewhat

divergent; corolla tube cylindrical, lobes spreading to reflexed, ovate, acutish, shorter than the tube, somewhat overlapping; scales nearly reaching the filaments, spatulate, fringed, bridged at from a quarter to a third of their height; anthers elliptical or oblong, sessile or subsessile; styles longer than the globose ovary. Capsule probably circumscissile, though not seen in fruit.

Type locality: San Luis Potosi, Mexico.

Specimens examined: MEXICO: *San Luis Potosi;* (Purpus 4972, 5444, the type, in the Univ. California Herb. as sheet 157,411).

Cuscuta choisiana n. sp.

[Figures 14 and 80]

Stems slender. Flowers 2.5–4 mm. long, waxy white and sometimes covered with white or transparent pellucid glandular appearing cells, nearly sessile, on pedicels as long as or mostly shorter than the flowers, clustered in compact clusters, each usually subtended by an ovate lanceolate bract; calyx lobes ovate-lanceolate, acute to acuminate, overlapping, about equalling the corolla tube, spreading somewhat at the tips; corolla cylindrical-campanulate; lobes upright to spreading, lanceolate, acuminate, about equalling the tube; scales reaching the filaments, fringed with medium length processes, bridged at about their middle; stamens slightly shorter than the lobes; anthers ovate, sagittate, versatile, some anthers showing apiculate connective; ovary globose-ovoid, slightly conical because of a thickening about the intrastylar aperture; styles slender, longer than the ovary, exserted; stigmas capitate. Capsule globose, circumscissile; seeds 2–4 in a capsule, ovate-globose, compressed, slightly oblique; hilum short, elliptical, oblique.

The name given this species is in honor of J. D. Choisy, the first botanist to mongraph the dodders.

Type locality: San Luis Potosi, Mexico. Range: Central Mexico.

Specimens examined: MEXICO: *San Luis Potosi;* San Luis Potosi (Purpus 4971, the type, in the U. S. Nat. Herb. as sheet 842,189), Chapala (Purpus 5036).

Cuscuta odontolepis Engelmann

C. odontolepis Engelmann, Trans. Acad. Sci. St. Louis, 1:486, 1859.

Stems slender. Flowers white, 3–5 mm. long, pentamerous, on pedicels shorter than the flowers in dense cymose paniculate clusters, usually with a broadly ovate, acute bract subtending one or several flowers; calyx shorter than or equalling the corolla tube, papillose-verrucose; lobes broad, ovate, deltoid, acute, overlapping; corolla cylindrical or campanulate, lobes shorter than or about equalling the tube, ovate, acute, upright to spreading or becoming reflexed, with or without a horn-like projection on the dorsal surface near the tip; scales large, oblong or somewhat spatulate, dentate about the upper portion only or fringed, shorter than the tube or reaching the filaments; stamens shorter than the lobes, anthers oblong

or oval, about equal to the filaments; styles slender, much longer than the globose ovary, becoming exserted in fruit; stigmas capitate. Capsule globose, thickened at the apex, readily circumscissile; seeds about 1.2 mm. long, light brown, generally four in each capsule, angled; hilum linear, oblique.

Cuscuta odontolepis typica

[Figures 7 a–d, 116 and 153]

Scales oblong, bridged at about a quarter of their height, shorter than the tube, denticulate at the truncated apex only, corolla cylindrical, lobes acute.

Type locality: Arizona. Range: Northern and central Mexico and Arizona.

Specimens examined: UNITED STATES: *Arizona;* (Wright 1624–529, the type, in the Engelmann Herb.), Santa Rita Forest Reserve (Griffiths & Thornber 21), Santa Rita Mts. south of Tucson (Engelmann in 1880).

MEXICO: *Sonora;* Fronteras (Hartman 52).

Cuscuta odontolepis fimbriata n. var.

[Figure 7 e]

Flowers shorter and campanulate; corolla lobes more obtuse, sometimes mucronate or with a dorsal projection; scales somewhat spatulate, bridged at about the middle, fringed with medium length processes.

Type locality: Papasquiaro, Durango, Mexico. Range: Central Mexico to Costa Rica.

Specimens examined: MEXICO: *Durango;* Papasquiaro (Palmer 412, the type, in the U. S. Nat. Herb. as sheet 304,596). *Guanajuato;* Guanajuato (Dugès in 1880).

COSTA RICA: (Warscewicz in 1848).

Cuscuta potosina Schaffner

C. potosina Schaffner in Watson, Proc. Amer. Acad. Arts & Sci., 18:124, 1883.

Stems slender. Flowers glabrous, about 2 mm. long, subsessile on pedicels shorter than the flowers in cymose panicles, commonly tetramerous or pentamerous, infrequently trimerous; calyx equal to or shorter than the corolla tube; lobes triangular acute; corolla campanulate or short cylindrical; lobes triangular acute, upright to slightly spreading, shorter than the tube; scales narrow, oblong, denticulate or fringed about the apex, shorter than the tube or reaching the filaments, bridged at about one-third their height; stamens shorter than the lobes, filaments slightly longer or shorter than the oval to roundish anthers; styles filiform, as long as or shorter than the globose somewhat ovate or depressed ovary; stigmas small, capitate. Capsule circumscissile with a small irregular opening, depressed-globose or ovoid, with the withered corolla at the apex or about it; seeds about 1mm. long, one to four in a capsule, but commonly only one, globose, flattened on one side, rounded on the other, finely punctated; hilum linear, oblique in a definite umbilical area of slightly darker color.

Cuscuta potosina typica
[Figures 28 a–f and 88]

Flowers commonly tetramerous. Corolla lobes connivent in fruit and corolla carried at the apex of the somewhat ovoid capsule; filaments about as long as or shorter than the anthers; scales scarcely reaching the filaments.

Type locality: Near San Luis Potosi, Mexico. Range: Central and southwestern Mexico.

Specimens examined: MEXICO: *San Luis Potosi;* San Luis Potosi (Schaffner 779, the type, in the Gray Herb.; 379). *Queretaro* (Rose, Painter & Rose 9650).

Cuscuta potosina globifera Schaffner, n. var.
[Figures 28 g–h and 87]

C. globifera Schaffner in herb.

Flowers larger, commonly pentamerous; filaments and scales longer. Capsule depressed-globose, surrounded by the withered corolla.

Type locality: Near San Luis Potosi, Mexico. Range: New Mexico and Arizona to central and southern Mexico.

Specimens examined: UNITED STATES: *New Mexico & Arizona Territory* (Rusby 295). MEXICO: (Pringle 7179). *San Luis Potosi;* San Luis Potosi (Schaffner 780, the type, in the Gray Herb.; 378). *Federal District* (Pringle 6575), Tlalpam (Rose & Rose 11215). *Puebla* (Purpus 5709).

Cuscuta partita Choisy
[Figures 12, 118 and 156]

C. partita Choisy, Mém. Soc. Phys. et Hist. Nat. Genève 9:284, pl. 5, fig. 3, 1841; and in DC., Prodromus, 9:460, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:487, 1859.—Progel in Martius, Fl. Brasiliensis, 7:386, pl. 128, fig. 6, 1871.

Stems rather slender. Flowers glabrous, about 1.5–2 mm. long, on pedicels about as long as the flowers, in dense cymose panicles; calyx loose about and more or less spreading away from the corolla; lobes triangular-acute; corolla deeply furrowed along the line of stamen attachment, the corolla bulging outward between the furrows; stamen attachment evident; corolla lobes spreading, triangular-acute, nearly as long as the tube; scales fimbriate, as long as the tube, bridged at about a third of their height; stamens shorter than the lobes; anthers oval or roundish, shorter than the filaments; styles filiform, longer than the globose ovary; stigmas capitate. Capsule globose, bulging in the four quarters about the developing seeds; seeds about 1.2 mm. long, four ordinarily produced in each capsule, round, compressed; hilum oblong, transverse.

Type locality: "Hab. in Brasiliâ apud Illheos." Type not seen. Range: Reported only from the Danish West Indies.

Specimens examined: WEST INDIES: (Boldingh 7081). *Curaçao* (Boldingh 5481, Britton & Shafer 2915).

Cuscuta desmouliniana n. sp.

Stems slender. Flowers slightly papillate, about 2 mm. long, mostly pentamerous or less frequently tetramerous, on pedicels as long as or longer

than the flowers; calyx lobes triangular or lanceolate, acute to acuminate, longer than the corolla tube and more or less spreading at the tips; corolla campanulate; lobes longer than the tube, erect to spreading and sometimes reflexed in fruit, lanceolate, acuminate; scales shorter than the tube, oblong, sparingly fringed with short processes about the upper part, or reduced to wings on either side of the filament attachment; stamens shorter than the lobes; filaments longer than the small, oval to oblong anthers; styles longer than the small, globose ovary; stigmas capitate. Capsule with the marcescent corolla at the apex, globose, thin, circumscissile, usually 3–4 seeded; seeds roundish, ovoid, about 1 mm. long, compressed, angled, hilum short, oblong, oblique.

This species is named in honor of Charles Des Moulins, one of the monographers of this genus.

Type locality: Hills near Altar, Sonora, Mexico.

Specimens examined: MEXICO: *Sonora;* Hills near Altar (Pringle 105, the type, in the Columbia College Herb. now at the N. Y. Bot. Gard.). This specimen seems to be a mixture of the following two distinguishable varieties.

Cuscuta desmouliniana typica n. var.

[Figures 25 a–e and 67]

Lobes of the calyx and corolla triangular-acute to acuminate; scales fully developed, fringed.

Cuscuta desmouliniana attenuiloba n. var.

[Figure 25 f–h]

Lobes of the calyx and corolla narrowly lanceolate, acuminate; scales reduced to wings on either side of the filament attachment.

Cuscuta umbellata Humboldt, Bonpland & Kunth

C. umbellata Humboldt, Bonpland & Kunth, Nov. Gen. Sp. Pl., 3:95, 1818.—Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:284, 1841; and in DC., Prodromus, 9:460, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:487, 1859.—Progel in Martius, Fl. Brasiliensis, 7:386, pl. 128, figs. 7 & 8, 1871.

C. parviflora Willdenow in Engelmann, Trans. Acad. Sci. St. Louis, 1:487, 1859; in synon.

Stems slender. Flowers glabrous or infrequently slightly puberulent, 2–6 mm. long, pentamerous, on pedicels longer or shorter than the flowers, forming rather dense compound cymes, the ultimate umbellate divisions of 3–7 flowers; calyx turbinate, as long as or longer than the campanulate corolla; lobes ovate-triangular, acute to acuminate; corolla lobes as long as or longer than the tube, reflexed, lanceolate or somewhat oblong, acute to acuminate; scales somewhat obovate or spatulate, moderately fringed with medium length processes, reaching the filaments or slightly exserted, or shorter in one variety, bridged at about a third or less of their height; stamens shorter than the lobes; anthers oblong to oval, shorter than or equalling the filaments; styles longer than the globose ovary; stigmas capitate. Capsule globose, depressed, with a ring or collar of thickened

knobs about the intrastylar aperture, circumscissile, surrounded by the withered corolla; seeds about 1 mm. long, angled, oblique, oval, yellowish; hilum oblong, linear, transverse.

Cuscuta umbellata typica
[Figures 9 a–e, 115 and 149]

Flowers usually not more than 3 mm. long; corolla lobes lanceolate, reflexed; scales ovate, as long as or longer than the tube.

Type locality: Between Queretaro and Salamanca, Mexico. Range: The southern United States, Mexico and the Greater Antilles.

Specimens examined: UNITED STATES: Foot of Rocky Mountains (James, on Long's exped.): *New Mexico;* (Stanley 7849, Wright 371, 1627, 1636, 1639, this number in Herb. Boissier=*C. leptantha typica*, Bigelow in 1851, Gregg, Mulford 1078a), Las Cruces (Wooton in 1895), Dona Ana Co. (Wooton in 1895 and in 1904, Wooton & Standley 3986), Socorro (Plank in 1895), Gila Valley (Green 12953), Gila (Schott), Gila River (Green in 1880). *Arizona;* Ft. Verde (Mearns in 1887, somewhat fleshy and puberulent), Santa Rita Grass Preserve (Goodding 2482), Beaver Creek (Purpus 8274), Prescott (Fernon 1896), San Pedro River (Hays). *Texas;* Laredo (Nealley 100, 100a, Mackenzie 81), southwestern Texas (Palmer 916), western Texas (Wright 510). *Colorado;* Fremont Co. (Brandegee 407). *California* (Lemmon). *Florida* (Garber 1883, Simpson 361, the flowers nearly sessile).

MEXICO: Mexico Boundary Line (Mearns 640). *Durango* (Pittier 497). *Chihuahua* (Palmer 500, Pringle 783). *Tamaulipas;* Victoria (Palmer 411, 501, 506, 511), Camargo (Gregg). *Oaxaca;* Cuicatlan (Rusby 129, somewhat fleshy puberulent). *Sonora* (Wright 695, Coulter 1010). *Puebla;* Tehuacan (Pringle 6297). *Coahuila;* Torreon (Palmer 471), Saltillo (Gregg 490), between Queretaro & Salamanca (Humboldt, the type, a fragment in the Engelmann Herb.).

WEST INDIES: *Cuba* (Wright 3107). *Porto Rico* (Britton & Shafer 1866, Britton, Cowell & Brown 4794), Punta Melones to Punta Casabe (Britton, Cowell & Brown 4676), Cayo Mertos (Britton, Cowell & Brown 4978). *Jamaica* (Broomfield in 1847, Britton 3102), Kingston (Britton & Hollick 1737).

Cuscuta umbellata reflexa (Coulter) n. comb.
[Figure 114]

C. californica reflexa Coulter, Contrib. U. S. Nat. Herb., 1:45, 1890.

Flowers large (4–6 mm. long), corolla lobes lanceolate, upright to reflexed; scales profusely fringed about the apex, spatulate, their lower half so firmly adherent to the tube as to render it difficult to detach for study. The large size of the flowers and compact clusters distinguish this variety.

Type locality: Roma, Texas. Range: Texas, Arizona and northern Mexico.

Specimens examined: UNITED STATES: *Texas;* Roma (Nealley 338, the type of *C. californica reflexa*, in the U. S. Nat. Herb. as type sheet 1,192). *Arizona;* San Carlos (Ebert in 1893), Tucson (Griffiths 2044, Thornber 8959, Engelmann in 1880).

MEXICO: *Lower California;* Cape region (Brandegee in 1902), west coast (Brandegee in 1893), Carduana (Brandegee in 1893). *Sinaloa;* Culiacan (Brandegee in 1904). *Sonora;* Pinacate Mts. (McDougal 26), Guaymas (Palmer 173).

Cuscuta umbellata dubia n. var.

[Figure 9 f–g]

Stems very slender. Flowers about 2 mm. long; calyx lobes triangular, acute, forming angles at the sinuses; corolla lobes about equal to the tube, spreading, triangular-oblong, acute.

This specimen, which is fragmentary, appears to be distinct. The stems are the most slender seen in any of the species.

Type locality: Guaymas, Sonora, Mexico.

Specimens examined: MEXICO: *Sonora;* Guaymas, on the sea beach (Palmer 1209, the type, in the U. S. Nat. Herb. as sheet 474,815).

Cuscuta gracillima Engelmann

C. gracillima Engelmann, Trans. Acad. Sci. St. Louis, 1:488, 1859.

Stems very slender, disappearing early from between the flower clusters. Flowers smooth or papillate, about 2 mm. long, on pedicels sometimes shorter but mostly longer than the flowers, in dense clusters; calyx turbinate; lobes triangular, lanceolate, acute to acuminate, longer than the tube of the corolla; corolla campanulate; lobes about as long as or slighty longer than the tube, triangular to lanceolate, acute; scales ovate, fringed, longer than the tube, or much reduced, bridged at about or below the middle; stamens longer or shorter than the lobes; filaments slender; anthers oblong, oval, somewhat versatile; ovary small, globose; styles capillary, many times the length of the ovary. Capsule tardily and irregularly circumscissile, depressed-globose, thin; seeds about 1 mm. long, one to four in a capsule, ovate, somewhat oblique; hilum oblong, oblique.

Cuscuta gracillima subtilis (Chaubard) n. comb.

[Figures 17 a–e and 82]

C. foetida Hooker & Arnott, Bot. Beechy Voy., p. 304, 1838; not HBK, 1818.

C. subtilis Chaubard in Engelmann, Trans. Acad. Sci. St. Louis, 1:489, 1859; in synon.

Flowers glabrous, pentamerous; scales well developed; stamens longer than the corolla lobes; the typical variety of the species.

Type locality: Mexico. Range: Central Mexico.

Specimens examined: MEXICO: A fragment of the type in the Engelmann Herb. *Jalisco;* Manzanillo (Palmer 949). *Sinaloa;* Mazatlan (Wright 1264, Rose, Standley & Russell 13727a, 13804). *Morelos;* Cuernavaca (Pringle 6189), valley near Yautepic (Pringle 8716).

Cuscuta gracillima esquamata n. var.

Flowers frequently tetramerous; scales lacking or reduced to but a few short processes; corolla somewhat glandular.

Type locality: El Taste, Lower California, Mexico.

Specimens examined: MEXICO: *Lower California;* El Taste (Brandegee in 1893, the type, in the Univ. California Herb.)

Cuscuta gracillima saccharata Engelmann

[Figures 17 f–g and 81]

C. gracillima saccharata Engelmann, Trans. Acad. Sci. St. Louis, 1:489, 1859.

C. sidarum Liebmann in Engelmann, Trans. Acad. Sci. St. Louis, 1:489, 1859; in synon.

Stamens not exceeding the corolla lobes; scales somewhat shorter than in var. *subtilis* but fully developed; flowers slightly smaller, densely papillose.

Type locality: Oaxaca, Mexico. Range: Southwestern Mexico.

Specimens examined: MEXICO: *Oaxaca* (Liebmann, taken as the type, a fragment in the Engelmann Herb.). *Guerrero;* Acapulco (Palmer 51, Herb. Le Jolis in 1866).

Cuscuta lacerata n. sp.

[Figure 18]

Stems slender. Flowers glabrous, pentamerous, about 2 mm. long, on pedicels as long as or longer than the flowers in dense, congested, paniculate cymes, the ultimate divisions umbellate; calyx exceeding the shallow, campanulate corolla; lobes somewhat uneven, lanceolate, acuminate, with scattered deep serrations; corolla lobes much exceeding the tube, lanceolate, acuminate, lacerated; scales exserted, somewhat spatulate, fringed, bridged at about a quarter of their height; stamens shorter than the lobes; anthers ovate-oblong, rather shorter than the slightly tapering filaments, somewhat versatile; ovary globose, slightly thickened at the apex; styles slender, much longer than the ovary. Capsule globose, with a slightly thickened collar about the intrastylar aperture; bearing the withered corolla about its apex; seeds one to four in a capsule, oval, somewhat compressed; hilum small, transverse?.

Type locality: Cuicatlan, Mexico.

Specimens examined: MEXICO: Cuicatlan (Smith 406, the type in the Gray Herbarium).

Cuscuta deltoidea n. sp.

[Figures 15 and 122]

Stems very slender. Flowers glabrous, pentamerous, short (mostly less than 2 mm. long), on pedicels much longer than the flowers in congested, cymose-paniculate clusters; calyx shallow; lobes short, broadly ovate, obtuse, overlapping, somewhat verrucose; corolla campanulate; lobes triangular-ovate, acute, becoming reflexed; scales shorter than the tube or reaching the filaments, fringed with medium length processes, bridged at about their middle; stamens slightly longer or about equalling the corolla lobes; anthers oval, shorter than the filaments, slightly versatile; styles longer than the globose ovary, becoming exserted; stigmas capitate. Capsule depressed-globose, with a thickened collar about the intrastylar aperture, circumscissile; mature seeds not seen.

This species differs from *C. gracillima*, which it resembles somewhat, in the more triangular-ovate corolla lobes and the short, broadly obtuse overlapping calyx segments. It differs from *C. pentagona* in its shorter scales, longer stamens, circumscissile capsule and type of inflorescence.

Type locality: Manzanillo, Jalisco, Mexico.

Specimens examined: MEXICO: *Jalisco;* Manzanillo (Palmer 948, the type, in the U. S. Nat. Herb. as sheet 208,677).

Cuscuta tuberculata Brandegee

[Figures 20 and 78]

C. tuberculata Brandegee, Univ. Calif. Bot. Publ., 3:389, 1909.

Stems slender. Flowers 2.5–4 mm. long, pentamerous, on pedicels longer or shorter than the flowers, in umbellate-racemose clusters; calyx about half as long as the cylindrical corolla tube; lobes triangular, acute, keeled, giving the calyx somewhat of a squarish appearance; corolla lobes equal to or shorter than the tube, upright, triangular-acute; the basal portion of the corolla papillate, especially that part enclosed by the calyx; scales about reaching the middle of the tube, ovate, fringed with short processes, bridged at about the middle; stamens shorter than the lobes or slightly longer in some specimens; anthers oblong, linear, shorter than or equalling the filaments; ovary small, globose, pointed, with a thickened ring about the intrastylar aperature; styles much longer than the ovary, exserted. Capsule globose, umbonate, circumscissile, with the withered corolla capping the capsule; mature seeds not seen.

Type locality: Santa Margarita island, Lower California, Mexico.
Range: Lower California to New Mexico.

Specimens examined: MEXICO: *Lower California* (Brandegee in 1915), Santa Margarita Island (Brandegee, the type, in the Univ. California Herb. as sheet 124,474), San José (Brandegee 404, Grabendorfer in 1899), Pescadero (Brandegee in 1893), west coast of cape region (Brandegee in 1893). *Sonora;* Northwestern Mts. (Pringle in 1884), Bavispe (Hartman 179).

UNITED STATES: *New Mexico;* Gila Valley (Green, 3 collections in 1880).

Cuscuta leptantha Engelmann

C. leptantha Engelmann, Trans. Acad. Sci. St. Louis, 1:489, 1859.

Stems very slender. Flowers 3–4.5 mm. long, tetramerous or pentamerous, on pedicels as long as or longer than the flowers, in umbellate clusters; calyx short, campanulate, lobes triangular-ovate, acutish, somewhat fleshy, papillose, about reaching the middle of the corolla tube; corolla cylindrical, fleshy and papillose in the basal portion; lobes nearly as long as the tube, upright to reflexed, slightly fleshy, triangular, lanceolate, acute; scales oblong, truncated or somewhat deltoid, shorter than the tube, fringed with short processes, bridged at about a quarter or a half of their height; stamens somewhat shorter than the lobes; anthers oval, shorter than the slender filaments; styles slender, much longer than the ovoid ovary, exserted; stigmas capitate. Capsule globose, slightly umbonate, two to four seeded, circumscissile, capped with the withered corolla; seeds about .8 mm. long, ovate, brown, oblique, compressed, angled; hilum short, oblique or transverse.

Cuscuta leptantha typica

[Figure 34 a–e]

Lobes of the corolla ordinarily four (infrequently five), upright; scales

oblong, truncated, sparingly fringed about the apex, bridged at about a quarter to a third of their height.

Type location: "Western Texas." Range: Texas and New Mexico to central Mexico.

Specimens examined: UNITED STATES: *Texas;* Western Texas to El Paso (Wright 522, taken as the type, in the Engelmann Herb.), Prairies of the Leona (Wright in 1852), Eagle Pass (Havard 4, Howard in 1888). *New Mexico;* (Wright 1639, in Herb. Boissier), Rio Gila (Green 275), Sierra Co. (Metcalf 1290)?.

MEXICO: *Sinaloa;* Culiacan (Rose, Standley & Russell 14929).

Cuscuta leptantha palmeri (Watson) n. comb.

[Figures 34 f and 91]

C. palmeri Watson, Proc. Amer. Acad. Arts & Sci., 24:64, 1889.

Lobes of the corolla usually five and reflexed; scales more deltoid and copiously fringed, bridged at about the middle.

Type locality: "At Los Angeles Bay, Lower California." Range: Lower California.

Specimens examined: MEXICO: *Lower California;* Los Angeles Bay (Palmer 544, the type, in the Gray Herb.), La Paz (Palmer 16, Brandegee 406).

Cuscuta polyanthemos Schaffner. n. sp.

[Figures 31 and 92]

C. polyanthemos Wilh. Schaffner in herb.

Stems very slender. Flowers glabrous, 4–5 mm. long, pentamerous or tetramerous, in umbellate clusters on pedicels usually two or more times the length of the flowers; calyx short, not over half as long as the corolla tube, its lobes triangular, acute; corolla tube 4–5 mm. long, cylindrical, slightly tapering towards the base; lobes triangular, lanceolate, acute, spreading to reflexed, about half as long as the tube; scales shorter than the tube, reaching about the middle, sparingly fringed with short processes, bridged at about one-third their height; stamens shorter than the lobes; anthers oblong-oval, shorter than the slightly subulate filaments; ovary globose, slightly pointed with a thickened collar about the intrastylar aperture; styles many times the length of the ovary, exserted; stigmas capitate. Capsule globose, slightly pointed, with the withered corolla carried at the apex, somewhat glandular, circumscissile, leaving the obcordate dissepiment in the calyx; seeds about 1 mm. long, usually four in each capsule, oval, angled; hilum oblong, oblique.

From *C. leptantha*, with which this species is closely allied, it differs mainly in the greater length of flowers and pedicels.

Type locality: Culiacan, Sinaloa, Mexico.

Specimens examined: MEXICO: *Sinaloa;* Culiacan (Schaffner, without date or number, the type, in the N. Y. Bot. Gard. Herb.; Brandegee in 1904 under the name of *C. palmeri*).

Section CLISTOGRAMMICA Engelmann

Cuscuta section Clistogrammica Engelmann, Trans. Acad. Sci. St. Louis, 1:491, 1859.

Capsule not circumscissile. Flowers with or without numerous subtending bracts. The species belonging to this section are those most commonly found in the United States. A small number of them are found in Canada, Mexico and the West Indies.

Key to the subsections

Flowers not subtended by bracts (sometimes present at the base of the flower cluster in *C. denticulata*); calyx segments more or less united.....PLATYCARPAE (p. 47).
Flowers subtended by numerous bracts; calyx segments mostly free...LEPIDANCHE (p. 72).

Subsection PLATYCARPAE Engelmann

Cuscuta § Platycarpae Engelmann, Trans. Acad. Sci. St. Louis, 1:491, 1859.
Cuscuta § Oxycarpae Engelmann, Trans. Acad. Sci. St. Louis, 1:499, 1859.

Flowers membranous or fleshy, mostly pedicellate, not subtended by numerous bracts (in *C. denticulata* one or two bracts may be present at base of the flower cluster).

Key to the species

Capsule globose, more or less depressed (pointed in *C. decipiens* and *C. indecora*); flowers membranous or fleshy; scales present.
Flowers mostly smooth, not particularly fleshy or papillate except in one variety.
Corolla remaining at the base of the mature capsule.
Corolla lobes obtuse; scales reaching the filaments; pentamerous.....*C. glandulosa* (p. 48).
Corolla lobes triangular, acute; scales reduced to a few processes about the apex; mostly tetramerous.....*C. polygonorum* (p. 49).
Corolla lobes acute, with inflexed tips; scales prominent; pentamerous.
Flowers about 2–3 mm. long, scales rather deeply fringed, exceeding the length of the tube.....*C. pentagona* (p. 50).
Flowers 2.5–5 mm. long, scales rather shallowly fringed, not reaching the filaments.....*C. plattensis* (p. 53).
Corolla carried at the apex of the capsule like a hood; mostly tetramerous.....*C. cephalanthi* (p. 53)
Corolla surrounding the capsule; calyx lobes not overlapping; pentamerous.
Calyx lobes not reaching the middle of the corolla, deltoid.....*C. racemosa chiliana* (p. 54).
Calyx lobes usually exceeding the middle of the corolla, ovate.....*C. decipiens* (p. 55).
Flowers fleshy, cells more or less lens shaped giving the flowers a slightly papillate appearance, tips of corolla lobes inflexed.
Flowers mostly tetramerous; scales rudimentary, represented by toothed wings.....*C. coryli* (p. 55).
Flowers mostly pentamerous; scales prominent.....*C. indecora* (p. 57).
Capsule globose or conic; scales represented by very short bridges and the slight beginning of a wing along the stamen attachent in some specimens.
Flowers fleshy, papillate; corolla lobes less than half as long as the corolla tube.....*C. jepsonii* (p. 59).
Flowers not fleshy; corolla lobes greater than half as long as the corolla tube.....*C. californica* (p. 60).

Capsule globose-ovoid to conic or long beaked; scales present, prominent, or but fringed wings along stamen attachment.
Flowers about 1 mm. long, frequently tetramerous; corolla lobes with inflexed tips.....
.....*C. harperi* (p. 63).
Flowers larger, nearly always pentamerous; corolla lobes not inflexed at the tips.
Capsule globose, flask-shaped with a long neck; flowers relatively large.....
..... *C. rostrata* (p. 63).
Capsule globose-ovoid or conic.
Calyx lobes ovate, obtuse, mostly even; capsule globose-ovoid, more or less pointed.
Capsule 3–5 mm. wide; scales ordinarily not truncated or bifid; styles usually at least one-third the length of the capsule. *C. gronovii* (p. 64).
Capsule 3–6 mm. wide; scales truncated or bifid; styles relatively shorter, usually about one-fourth the length of the capsule.. *C. curta* (p. 67).
Calyx lobes orbicular, denticulated; capsule globose-ovoid.....
.....*C. denticulata* (p. 68).
Calyx lobes deltoid or lanceolate, acute to acuminate.
Scales reaching the filaments, bridged at about the middle.....
.....*C. veatchii* (p. 69).
Scales shorter than the tube, shallowly fringed or reduced to wings, bridged below the middle.
Calyx lobes shorter than the tube, overlapping; flowers 5–6 mm. long.....*C. subinclusa* (p. 69).
Calyx lobes equalling the tube, not overlapping; flowers 2–4.5 mm. long.....*C. salina* (p. 70).

Cuscuta glandulosa (Engelmann) Small
[Figures 41, 125 and 143]

C. glandulosa (Engelmann) Small, Flora So. East. U. S., p. 969, 1903.
C. obtusiflora glandulosa Engelmann, Trans. Acad. Sci. St. Louis, 1:492, 1859.

Stems medium. Flowers glabrous, about 2 mm. long, pentamerous, subsessile to sessile in globular, compact clusters; calyx shorter than or nearly as long as the corolla tube; lobes ovate, obtuse, slightly overlapping; corolla campanulate; lobes shorter than the tube, ovate, obtuse, upright to spreading, often becoming reflexed as the fruit matures; scales as long as the tube, fimbriate, prominent, or somewhat shorter and slightly bifid; stamens shorter than the lobes; filaments longer than the oval anthers and somewhat subulate; styles longer than or equal to the globose ovary. Capsule depressed-globose, angled by the developing seeds; seeds ordinarily two to four in each capsule, brown, oval; hilum oblique or transverse and at one side, oblong.

The whole flower is more or less dotted with glandular-like cells and reddish. This species, which in many respects resembles *C. polygonorum*, differs in the pentamerous flowers, with more prominent scales and in the obtuse corolla lobes.

Type locality: Georgia. Range: Throughout the southern United States from California to Florida and in the Greater Antilles and northern Mexico.

Specimens examined: UNITED STATES: *Texas;* San Marcos (Nealley 92), Dallas (Reverchon in 1878), Rio San Pedro (Bigelow in 1850, Schott in 1851), western Texas to El Paso (Wright in 1849). *California;* San Bernardino Co. (Parish), San Bernardino (Parish in 1898). *Indian Territory;* Sapulpa (Bush 1405). *Louisiana* (Tainturier; Langlois 237). *Georgia* (Boykin in 1838, taken as the type, in the Engelmann Herb.). *Florida* (Rugel 400), Jamony (Rugel in 1843), St. George's Island (herb. Chapman in 1863).

WEST INDIES: *Porto Rico;* Sierra de Naguabo (Britton, Britton & Cowell 2109). *Cuba* (Wright in 1865, van Hermann 686); Habana (Wilson 1111, 1129).

MEXICO: *Durango;* Durango (Palmer 605).

Cuscuta polygonorum Engelmann
[Figures 39, 107 and 150]

C. polygonorum Engelmann, Amer. Journ. Sci. & Arts, 43:342, pl. 6, figs. 26–29, 1842.—Choisy in DC., Prodromus, 9:461, 1845; not Cesati, 1849.

C. chlorocarpa Engelmann in Gray, Manual of Botany, p. 350, 1848; and Trans. Acad. Sci. St. Louis, 1:494, 1859.—Britton & Brown, Illustr. Flora, 3:28, fig. 2959, 1898; and 2 ed., 3:49, fig. 3445, 1913.—Matthew, Bull. Torr. Bot. Club, 20, pl. 165, fig. 7, 1893.

Stems medium to slender. Flowers glabrous, about 2–2.5 mm. long, mostly tetramerous (infrequently tri- or pentamerous), subsessile, in compact, dense, glomerulate clusters; calyx lobes triangular, obtuse, as long as or longer than the corolla tube, corolla short campanulate, lobes triangular-acute, upright, as long as or slightly longer than the corolla tube; scales oblong, about reaching the filaments or shorter, bifid, their processes few and short, about the upper portion, bridged at about a quarter of their height; stamens shorter than the lobes; anthers oval, pollen sacs sometimes separated by the connective, shorter than the subulate filaments which are situated more or less directly in the sinuses; styles shorter than the globose, depressed ovary, becoming subulate and divergent. Capsule globose, depressed, appearing cubical about the developing seeds; intrastylar aperture large, rhombic; seeds about 1.3 mm. long, yellowish brown, roundish, slightly rostrate and compressed; hilum oblong, linear, transverse to oblique.

Type locality: "West of St. Louis." Range: From Maryland and the District of Columbia west to Minnesota and Nebraska and south to Tennessee and possibly to Texas.

Specimens examined: UNITED STATES: *Maryland;* Little Falls of Potomac (Mohr in 1882), Glen Echo (Hillman), Chesapeake Bay region (Shull 393). *Delaware* (Tatnall). *District of Columbia;* Washington (Chase 2532, Steele in 1900). *Pennsylvania;* Lancaster Co. (Porter in 1863). *Ohio;* Ottawa Co. (Moseley in 1898), Florence (Moseley in 1897), *Kentucky;* Bowling Green (Price in 1898), Harlan Co. (Lloyd in 1888). Crawford Co. (Sears in 1916). *Tennessee;* Nashville (Gattinger in 1881). *Indiana;* Whiting (Hill in 1891), Hanover (Coulter in 1876), Grant Co. (Deam 15269), Franklin Co. (Deam in 1903), Vigo Co. (Deam 22182). *Illinois;* Elgin (Umbach in 1895), Mt. Carmel (Schneck in 1905, in 1897, on Pataka Island near Mt. Carmel in 1879 and one collection without date), Peru (Engelmann in 1840, taken to represent the type, in the Engelmann Herb.), Wabash Co. (Schneck in 1880). Urbana (Clinton 30438, Yuncker 1010, 1000a, b, c, & d), Taylorville (Andrews in 1892 and in 1898), Peoria (Brendel in 1892), St. Clair Co. (Eggert in 1878). *Wisconsin;* Green Bay marsh east of Fox River (Schuette 95–11–7), Beaver Dam (Chandler 485), Madison (Cheney

in 1889). *Minnesota;* Winona (Holzinger in 1888). *Nebraska;* Exeter (Wibbe in 1889, in part), Lincoln (Hannah in 1916). *Kansas;* Riley Co. (Norton 358).

Cuscuta pentagona Engelmann

C. pentagona Engelmann, Amer. Journ. Sci. & Arts, 43:340, pl. 6, figs. 22–24, 1842.—Choisy in DC., Prodromus, 9:461, 1845.

C. arvensis Beyrich in Hooker, Fl. Bor. Am., 2:77, 1838; as synonym without description.—Engelmann in Gray, Manual of Botany, (2 ed.), p. 336, 1856; and in Trans. Acad. Sci. St. Louis, 1:494, 1859.—Hillman, Nev. Agr. Exp. Sta. Bull., No. 15, fig. 4, 1892.—Matthew, Bull. Torr. Bot. Club, 20, pl. 164, fig. 3, 1893.—Piper, Wash. Agr. Exp. Sta. Bull., No. 8, fig. 2, 1893.—Britton & Brown, Illustr. Flora, 3:28, fig. 2958, 1898; and 2 ed. 3:49, fig. 3444, 1913.

Epithymum arvense (Beyrich) Nieuwland & Lunell, Amer. Mid. Nat., 4:511, 1916.

Stems slender. Flowers 2–3 mm. long, glabrous to papillate or verrucose, pentamerous, on pedicels as short as or longer than the flowers in dense globular clusters; calyx lobes broad, obtuse, sometimes overlapping and angled; corolla broad, campanulate, lobes as long as or slightly longer than the tube, reflexed or spreading, with the tips acute and inflexed; scales longer than the tube, broad, ovate, deeply fringed, particularly the upper portion; stamens shorter than the lobes; anthers shorter than the filaments, slightly versatile, ovoid, elliptical; styles as long as or slightly longer than the globose ovary. Capsule globose, more or less depressed, the withered corolla remaining at the base; seeds 1–1.2 mm. long, light brown, usually four in a capsule, obovate or oval, compressed; hilum short, linear, oblique or transverse.

Key to the varieties

Calyx lobes overlapping, forming angles at the sinuses; flowers relatively small..... *typica.*
Calyx lobes not at all or but slightly overlapping and not forming angles at the sinuses; flowers usually larger.
  Flowers smooth, not verrucose or pubescent..... *calycina.*
  Flowers more or less verrucose or pubescent.
    Flowers more or less verrucose..... *verrucosa.*
    Flowers papillose-pubescent..... *pubescens.*

Cuscuta pentagona typica
[Figures 33 a–e, 112 and 127]

C. pentagona microcalyx Engelmann, Amer. Journ. Sci. & Arts, 45:76, 1845.

C. arvensis pentagona Engelmann, Trans. Acad. Sci. St. Louis, 1:494, 1859.

C. globularis Nuttall in Engelmann, Trans. Acad. Sci. St. Louis, 1:494, 1859; in synon.

Smallest of the varieties. Calyx lobes smooth, roundish-triangular, overlapping at the sinues forming angles.

Type locality: Norfolk, Virginia. Range: From Massachusetts to Florida and west to California.

Specimens examined: UNITED STATES: Fort Smith to the Rio Grande (Bigelow 1, 9). *Massachusetts;* Winchester (Bartlet 691, 696, Fernald & Weatherby 259, Rich in 1896), Cambridge (Weatherby in 1911). *Connecticut;* Oxford (Harger in 1891), Simsbury (Bissell in 1904). *District of Columbia;* Washington (Blanchard in 1890, Hillman in 1904, Holm in 1893), Eckington (Boettcher 122), Takoma Park (Painter 745). *New Jersey* (Van Sickle in

1894), Landisville (Gross in 1882), Cape May (Martindale in 1877), Cumberland Co. (Parker in 1866), Ocean Co. (Mackenzie 4782). *Virginia;* Suffolk (Kearney 1583), Luray (Steele 155), Lake Smith (Hitchcock in 1905), Norfolk (Hitchcock in 1905), Bedford Co. (Curtiss 5840). *New York;* Long Island (Bisky in 1886). *Pennsylvania;* Susquehanna (Ely in 1888). *Delaware* (Canby in 1863), Townsend (Chickering in 1873), Wilmington (Canby in 1895), Pencader (Tatnall in 1884). *Maryland;* Spencerville (Bond in 1891), Crisfield (Holmes 17188), College Park (Blodgett in 1903). *N. Carolina* (Beyrich in 1845, the type? of *C. arvensis* in the Engelmann herb. McCarthy in 1885, Ashe, Thaxter in 1887), Hillsborough (Curtiss in 1843), Beaufort (Lewis 224). *S. Carolina* (Ravenel), Aiken (Ravenel in 1869). *Florida* (Rugel 400a, 400b), St. Marks (Rugel in 1843), Jacksonville (Keeler in 1889, Curtiss 2188), Brevard Co. (Nash 2283), Penscacola (Mohr in 1874), Carrabelle (Curtiss 5881), Biscayne Bay (Chapman), St. Augustine (Reynolds in 1872). *Alabama;* Mobile (Mohr in 1888), Valley Head (Ruth 477, 492). *Georgia;* DeKalb Co.(Eggert in 1897, Small in 1893), Whitfield Co. (Wilson 138), Stone Mt. (Engelmann in 1876). *Mississippi* (Tracy in 1892). *Tennessee* (Gattinger in 1879), Cocke Co. (Kearney 843), Nashville (Killebrew in 1885), Knoxville (Ruth 169), Rutherford (Eggert in 1897). *Kentucky;* Bowling Green (Price in 1898). *Indiana;* Gibson Co. (Schneck in 1906), Ripley Co. (Deam 7101), Vermilion Co. (Deam 9871), Orange Co. (Deam 17384), Spencer Co. (Deam 28370, 28400), Posey Co. (Deam 25430), Bartholomew Co. (Deam 12403). *Illinois;* Peoria (McDonald in 1904), Freeport (Johnson in 1900), Beardstown (Geyer in 1842, the type of *C. pentagona microcalyx*, in the Engelmann Herb.), Henderson Co. (Patterson), Cook Co. (Beal in 1869), West Pullman (Lansing 2846), Oregon (Hill 128–1905), Kankakee (Hill 76–1871), Glencoe (Eggert in 1879). *Minnesota;* Minneapolis (Sheldon in 1891). *S. Dakota* (Skinner 200), Bad Lands (Williams in 1891), Custer (Coulter in 1874), Pennington Co. (Over 1907). *Nebraska* (Hayden in 1853–54), Ewing (Bates 698). *Iowa;* Ames (Hitchcock). *Missouri;* Eagle Rock (Bush 36), Lee's Summit (Bush 138), St. Louis (Eggert in 1879), Springfield (Standley 8980), Dent Co. (Tracy 17189), Iron Mt. (Trécul in 1848), Hillsborough (Riehl in 1848), Allentown (Letterman in 1875), Jefferson Co. (Eggert in 1891, and in 1896), Webb City (Palmer 432), St. Francis Co. (Russell in 1897), Taney Co. (Eggleston 12247), Willard (Blankinship in 1889), Malden (Bush in 1893), Shannon Co. (Bush 1007; 1062), McDonald Co. (Bush in 1892). *Indian Territory;* Cickasaw Nation (Sheldon in 1891), Colbert's Station (Sheldon 21). *Colorado;* Paradox (Walker 348). *Montana;* Glendine (Ward in 1883). *California;* Antioch Kellogg & Harford 780).

Cuscuta pentagona calycina Engelmann
[Figures 33 f–g and 113]

C. pentagona calycina Engelmann, Amer. Journ. Sci. & Arts, 45:76, 1845.
C. arvensis calycina Engelmann, Trans. Acad. Sci. St. Louis, 1:495, 1859.

Flowers larger; calyx lobes ovate or roundish, shorter than or longer than the corolla, not at all or but slightly overlapping and not angled at the sinuses.

Type locality: Texas. Range: From Virginia to the Greater Antilles and westward to Saskatchewan, Manibota, California, Texas and northern Mexico.

Specimens examined: UNITED STATES: (Wooton 2749), Lat. 41° (Harbour 464). *Virginia;* Nansemond Co. (Heller 1135). *Tennessee;* Knoxville (Ruth in 1893). *Indiana;* Clarke (Umbach in 1898). *N. Dakota;* Big Stone Lake (Griffiths & Slosser 235). *S. Dakota;* Brookings (White), Fall River Co. (Visher 2596). *Nebraska;* Scotts Bluff Co. (Rydberg 264). *Missouri;* Courtney (Bush 3013, 5855), Carthage (Bush & Palmer 3063), Kansas City (Bush 1750, 4068). *Kansas;* Manhattan (Kellerman 50). *Arkansas;* Eureka Springs

(without designation of collector, in 1898). *Colorado;* Grand Junction (Hedgcock in 1901), Boulder (Daniels 696), Naturita (Payson 588). *Nevada;* Reno (Hillman). *Montana;* Bozeman (Blankinship 407). *Utah* (Jones 5482b, 5653, Eastwood 91, Rydberg & Garrett 9918, 10013, 10014, Hedrick in 1899), Salt Lake City (McKinney in 1916). *Washington;* Waitsburg. (Horner 639). *Oregon;* Mouth of the Walla Walla River (Geyer 674), Multnomah Co. (Howell 336). *California;* Santa Clara Co. (Abrams 2230, Baker 1761), San Jose (Rattan 4d), Redondo (Grant in 1901, McClatchie in 1892), southern California (Grant 3629). Mariposa (Congdon in 1902), Bouldin Island (Brandegee). *Arizona* (Rusby 245, 295), Camp Lowell (Rothrock 708), Tucson (Pringle 144, 13797, and in 1891), Solomonville (Goodding 509), Flagstaff (McDougal 378), Ash Creek (Rothrock 311), Cosnino (Jones 4032). *New Mexico* (Rusby 85, and in 1880), Frisco River (Wooton in 1900), Chavez (Wooton in 1892), Dona Ana Co. (Wooton & Stanley 3988 and in 1906), Mangas Springs (Metcalf in 1903), Alberque (Jones 4116 and in 1884, Herrick in 1904), La Luz (Wooton in 1905), San Juan Co. (Standley 6958). *Texas* (Thuron in 1890, Lindheimer 664, 126, taken as the type, in the Engelmann Herb., Wright in 1847), Dallas (Reverchon in 1880), Concho (Havard 2), San Marcos (Stanfield in 1898).

CANADA: *Assiniboia* (Macoun 11852). *Saskatchewan* (Drummond). *Manitoba;* Morris (Macoun 23972).

MEXICO: *Jalisco* (Pringle 3111). *Chihuahua;* Santa Rosalia (Palmer 382). *Lower California;* San Jorge (Brandegee 4), Baja (Brandegee).

WEST INDIES: *Cuba;* Havana (Leon 7707, Leon & Eckman 4270). *Bahamas;* Andros (Wight 228). *Jamaica;* Claredon (Britton 3798). *Porto Rico;* Arecibo to Utuado (Britton & Cowell 306).

Cuscuta pentagona verrucosa (Engelmann) n. comb.

[Figure 111]

C. verrucosa Engelmann, Amer. Journ. Sci. & Arts, 43: 341, pl. 6, fig. 25, 1842.—Choisy in DC., Prodromus, 9:461, 1845.

C. verrucosa glabrior Engelmann, Amer. Journ. Sci. & Arts, 43:341, 1842.

C. arvensis verrucosa Engelmann, Trans. Acad. Sci. St. Louis, 1:495, 1859.

Pedicels usually longer than in the other varieties, equalling the flowers or longer; calyx lobes more triangular, obtuse, usually shorter than the corolla, fleshy verrucose; capsule somewhat verrucose to papillate.

Type locality: Texas. Range: Louisiana, Indian Territory, Texas and northern Mexico.

Specimens examined: UNITED STATES: *Louisiana;* Sulphur (Palmer 7709). *Indian Territory;* Limestone Gap (Butler 4), Between Fts. Cobb & Arbuckle (Palmer 202). *Texas* (Drummond III 247, taken as the type in the Engelmann Herb., Ruth 502, Lindheimer 127, 473), Corpus Christi (Heller 1549) Dallas (Reverchon in 1878, Hall 492, 493 in part), Galveston island (Joor in 1877), San Antonio (Palmer 12914, Larrabee in 1900).

MEXICO: (Berlandier 2457). *Coahuila* (Palmer 723), Saltillo (Palmer 218, 307, 730), Parras (Gregg 401, 417). *San Luis Potosi;* San Luis Potosi (Berlandier in 1827). *Coahuila & Nouvo Leon* (Palmer 919).

Cuscuta pentagona pubescens (Engelmann) n. comb.

C. arvensis pubescens Engelmann, Trans. Acad. Sci. St. Louis, 1:495, 1859.

All parts of the flower more or less papillate-pubescent.

Type locality: Western Texas. Range: New Mexico and Texas.

Specimens examined: UNITED STATES: *New Mexico* (Wright 1631, 1635). *Texas* (Wright 2, Lindheimer in 1847, taken as the type, in the Engelmann Herb.), El Paso (Wright 519, 523), Bexar Co. (Jermy 34) Llano Co. (Nealley 84), on the Pedernales river (Lindheimer in 1847), along the Pecos. (Wright 574.)

Cuscuta plattensis Nelson
[Figure 35]

C. plattensis Nelson, Bull. Torr. Bot. Club, 26:131, 1899.

Stems medium to slender. Flowers glabrous, 2.5–5 mm. long, pentamerous, on pedicels about equal to the flowers in panicled cymes; calyx shorter than the corolla tube; lobes triangular, obtuse, slightly overlapping; corolla tube broadly campanulate; lobes about equalling the tube, triangular, acute, (not "short-ovate, obtuse, about half the length of the broadly campanulate tube"), slightly irregular in some, spreading or reflexed, with the tips inflexed; scales shorter than the tube, slightly spatulate, copiously fringed with short processes; stamens shorter than the lobes; anthers oval, about equal to the subulate filaments; ovary depressed-globose, verrucose and thickened about the intrastylar aperture; styles slightly unequal, about equal to the ovary or shorter. Capsule depressed-globose; seeds one to four in a capsule, about 1–1.5 mm. long, oval or obovate, robust; hilum short, linear, transverse.

This species is very closely related to *C. pentagona* and perhaps merges with some of the larger forms of variety calycina. It seems to differ in the shorter scales and shorter processes and the rather larger flowers.

Type locality: "In cañon of Platte," Wyoming. Range: Wyoming and Washington.

Specimens examined: UNITED STATES: *Wyoming;* Platte Canyon (Nelson 2768, the type, in the Rocky Mt. Herb., Univ. of Wyoming), Uva (Nelson 2741, mixed with *C. indecora* on some sheets), Converse Co. (Nelson 9118). *Washington;* Klickitat Co. (Suksdorf 2852.)

Cuscuta cephalanthi Engelmann
[Figures 53, 57, 58 and 142]

C .cephalanthi Engelmann, Amer. Journ. Sci. & Arts, 43:336, pl. 6, fig. 1–6, 1842.—Matthew, Bull. Torr. Bot. Club, 20, pl. 164, fig. 6, 1893.—Britton & Brown, Illustr. Flora, 3:29, fig. 2962, 1898; 2 ed., 3:50, fig. 3448, 1913.

C. tenuiflora Engelmann in Gray, Manual of Botany, p. 350, 1848; and in Trans. Acad. Sci. St. Louis, 1:497, 1859.

Epithymum cephalanthi (Engelmann) Nieuwland & Lunell, Amer. Mid. Nat., 4:511, 1916.

Stems medium. Flowers glabrous, about 2 mm. long, commonly tetramerous, less frequently tri- or pentamerous, sometimes more or less glandular; calyx shorter than the corolla tube, deeply divided; lobes oblong-ovate, obtuse; corolla cylindric-campanulate, becoming somewhat urceolate as the capsule matures; lobes ovate, obtuse, erect to spreading, much shorter than the tube; scales oblong, narrow, fringed with scattered processes, reaching the filaments, bridged at from a quarter to a third of their height; stamens mostly equal to or slightly shorter than the lobes; anthers oval to round, about equal to the stoutish filaments; styles equal to or slightly longer than the globose somewhat depressed ovary. Capsule depressed-globose, capped by the persistent, withered corolla; seeds about

1.6 mm. long, light brown, globose, ovate or round, slightly oblique and compressed; hilum oblong, linear, oblique.

This species in some respects resembles the smaller forms of *C. gronovii* but is separable by the ordinarily tetramerous flowers and the depressed, capped capsule.

Type location: "On the margins of ponds and swamps near St. Louis." Range: Across the continent from Maine to Oregon and Washington and southward to Virginia, Tennessee and Texas.

Specimens examined: UNITED STATES: Near 49th parallel of lat. (Lyall in 1858–59). *Maine;* Orono (Briggs 1509). *Massachusetts;* Framingham (Sturtevant in 1890). *Connecticut;* Waterbury (Dubois in 1888), Greens Farms (Polard 239). *New Jersey* (Engelmann in 1879, Canby in 1862). *Virginia;* Little Falls of the Potomac (Mohr in 1894). *New York;* Cayuga Lake (Dudley in 1882, Wiegand in 1895), west New York swamps (Van Sickle in 1894). *Pennsylvania;* Marysville (Small in 1888), Lancaster Co. (Porter in 1864), Easton (Porter in 1890 and in 1895), Harrisburg (Porter in 1879). *Tennessee* (Gattinger in 1886). *Ohio;* Port Clinton (Mosely in 1897), Erie Co. (Mosely in 1898), Painesville (Beardslee in 1876), Cincinnati (Lloyd in 1890). *Michigan;* Jackson (Camp in 1893), Algonac (Cooper in 1901). *Indiana;* Clarke (Umbach in 1898), Dune Park (Chase 1982), Whiting (Hill in 1891), Wells Co. (Deam 490, in 1899, 1903 & 1905)., Adams Co. (Deam 5363, 5364 in part), Porter Co. (Deam 26482), Parke Co. (Deam 9889), Carroll Co. (Deam 15304), Allen Co. (Deam 1582), Randolph Co. (Deam 15382), Steuben Co. (Deam 15476). *Illinois;* Wabash Co. (Schneck in 1880), Peoria (McDonald in 1885 and in 1894, Brendel), Ravinia (Sherff in 1911), Vermillion Co. (McDougall in 1917), Oquawka (Patterson), Henderson Co. (Patterson 10430 and in 1872), Carlinville (Andrews in 1890), Libertyville (Sherff 1896), Athens (Hall in 1861 and in 1867), Taylorville (Andrews in 1898), Sangamon Co. (Andrews in 1898), Beardstown (Geyer), Ringwood (Vasey in 1861), Urbana (Pease, Yuncker 999a, 999b, Clinton 11794, 11795, 11796, 28574, 30449, 30450). *Wisconsin;* Osceola (Sheldard in 1892), Brown Co. (Schuette in 1894), Winnebago Co. (Kellerman in 1871), Racine (Davis in 1879), Prairie du Chien (Hall in 1861), Madison (Hall in 1861). *Minnesota;* Winona (Holzinger in 1889), Yellow Medicine Co. (Jacobs in 1888), Glyndon (Dewart in 1892). *Iowa;* Fayette Co. (Fink 207, 632), Ames (Hitchcock in 1894), Vinton (Davis in 1876). *Missouri;* St. Louis (Engelmann in 1841, taken as the type, in the Engelmann Herb., also in 1842 and in 1860), Clark Co. (Bush in 1892), Jackson Co. (Bush 262). *Kansas;* Lawrence (Stevens). *Nebraska;* Lawsville (Williams in 1888), Exeter (Wibbe in 1889 in part), Nickolls Co. (Hedgcock in 1894), Banks of the Missouri river (Hayden). *Nevada;* Humboldt Pass (Watson 937). *Utah;* Salt Lake City (Jones 1918, Garrett 2213), Ogden (Tracy in 1887). *Oregon;* Hood river (Henderson in 1884). *Washington;* Klickitat Co. (Suksdorf in 1883). *California;* Mt. Shasta (Grant 5217). *New Mexico* (Wright 1626=578, 1629=124), Otero Co. (Wooton in 1899). *Texas;* Dallas (Reverchon in 1878).

Cuscuta racemosa chiliana Engelmann
[Figures 36 and 94]

C. racemosa chiliana Engelmann, Trans. Acad. Sci. St. Louis, 1:505, 1859.

No North American synonymy; for foreign synonymy see Engelmann, Trans. Acad. Sci. St. Louis, 1:505, 1859.

Stems slender to medium. Flowers glabrous, about 3 mm. long, pentamerous, on pedicels as long as or mostly longer than the flowers in loose, racemose cymes; calyx much shorter than the corolla tube; lobes short, deltoid, acute; corolla campanulate; lobes shorter than the tube, spreading

to reflexed, triangular-ovate, acutish; scales scarcely reaching the filaments, fringed, bridged at about a quarter of their height; stamens about equalling the lobes; anthers oval-oblong, about equal to the somewhat subulate filaments; ovary globose; styles slender, rather longer than the ovary. Capsule globose, glandular, thin, not thickened but somewhat verrucose at the top; styles slightly tapering towards the base; seeds two to four in a capsule, about 1.5 mm. long, roundish, compressed, somewhat rostrate; hilum small, depressed.

Type locality: Chile. Type not seen. Range in North America: Scattered across the continent, mostly on *Medicago sativa.*

Specimens examined: UNITED STATES: *Maryland;* near Baltimore (Hillman). *S. Dakota;* White River (Over 2355). *Texas;* Sanderson (Wooton in 1911). *California;* Kern Co. (Palmer 149), lower Sacramento (Jepson in 1893), Santa Cruz Mts. (Davis in 1908). northern California (Greene 1046).

Cuscuta decipiens n. sp.
[Figures 43, 93 and 95]

Stems slender. Flowers about 3 mm. long, glabrous, pentamerous, subsessile or on pedicels as long as or slightly longer than the flowers; calyx lobes ovate, obtuse, somewhat shorter than the corolla tube; corolla campanulate, its lobes triangular-ovate, somewhat serrate, obtuse, or acute with an inflexed tip; scales as long as or shorter than the tube, deeply fringed, slightly spatulate, bridged at about a third of their height; stamens shorter than the lobes; filaments about equal to the oval anthers; ovary globose, slightly umbonate; styles slender, shorter than the ovary; stigmas capitate. Capsule globose-oval, slightly umbonate, with the withered corolla about it; seeds usually one or two in a capsule, about 1.7 mm. long, light brown or yellow, rostrate or hooked; hilum linear, oblong, oblique or transverse, the umbilical area scarcely contrasted with the rest of the seed.

All parts of the flowers are white or reddish and covered with numerous whitish pellucid glandular-appearing cells. This species resembles *C. indecora*, but is distinguishable by its obtuse calyx lobes, less fleshy and smooth flowers, with scales which are ordinarily shorter, as well as by the capsule which is not thickened as much at the apex.

Type locality: Hacienda de Cedros, Zacatecas, Mexico. Range: Central Mexico.

Specimens examined: MEXICO: *Zacatecas;* Hacienda de Cedros (Lloyd 193, the type, in the U. S. Nat. Herb. as sheet 574,160), Hilo de Oro (Lloyd 28), Cedros (Kirkwood 50). *Coahuila* (Purpus 4873).

Cuscuta coryli Engelmann
[Figures 42, 55, 56 and 130]

C. coryli Engelmann, Amer. Journ. Sci. & Arts, 43:337, pl. 6, figs. 7–11, 1842.—Matthew, Bull. Torr. Bot. Club., 20, pl. 164, fig. 5, 1893.—Britton & Brown, Illustr. Flora, 3:29, fig. 2961, 1898; 2 ed., 3:50, fig. 3447, 1913.—Stevens, Amer. Journ. Bot., 3:185, figs. 1–2, 1916.

C. compacta crenulata Choisy in DC., Prodromus, 9:459, 1845.
C. inflexa Engelmann, Trans. Acad. Sci. St. Louis, 1:502, 1859.
C. congesta Beyrich; *C. parviflora* Nuttall; *C. umbrosa* Beyrich, herb. names without descriptions in Engelmann, Trans. Acad. Sci. St. Louis, 1:502, 1859; in synon.
Epithymum coryli (Engelmann) Nieuwland & Lunell, Amer. Mid. Nat., 4:511, 1916.

Stems medium to slender. Flowers fleshy, papillate, about 2 mm. long, mostly tetramerous (less frequently penta- or trimerous), on pedicels shorter or longer than the flowers, in panicled cymes; calyx lobes triangular, acute, equalling the corolla tube; corolla cylindric-campanulate; lobes triangular-ovate, crenulate, upright, with acute inflexed tips; scales rudimentary, bifid, toothed, ordinarily reduced to toothed wings on either side of the filament attachment, bridged somewhat below the middle; stamens about as long as the lobes; anthers oval to slightly oblong, on somewhat subulate filaments; ovary globose-ovoid, thickened at the apex; styles shorter than or equal to the ovary, becoming widely divergent on the capsule. Capsule at first globose, becoming depressed, thickening in a collar about the intrastylar aperture, the withered corolla about the upper part or soon falling away; seeds about 1.5 mm. long, usually four in each capsule, dark brown, globular or somewhat compressed, rather oblique, the surface scurfy; hilum short, oblong, oblique or transverse.

This species resembles *C. indecora* but differs in its ordinarily tetramerous flowers, rudimentary scales, more compressed capsule and more widely divergent styles.

Type locality: In dry prairies near St. Louis. Range: From Rhode Island and Virginia westward to South Dakota, Nebraska and Montana and southward to Texas and Arizona.

Specimens examined: UNITED STATES: Left Bank of Missouri (Ward in 1883). Bluffs of the Cumberland (Ward in 1877). (Nuttall in Herb. Acad. Phil., the type of *C. parviflora*, a fragment in the Engelmann Herb.). *Rhode Island;* Smithfield (Olney in 1872). *Delaware;* Harrington (Canby in 1886). *Virginia* (Gray & Sullivant in 1843), Peak of Otter (Beyrich, the type of *C. congesta*, a fragment in the Engelmann Herb.). *Maryland;* Piney Point (Vasey in 1873), Glen Echo (Hillman in 1904 and in 1905). *New York;* Staten Island (Burnham in 1901), Washington Co. (Burnham in 1895), Ithaca (Dudley in 1882), Peekskill (Leggett in 1870), Niagara Co. (Clinton in 1864). *Tennessee;* (Beyrich 175–2, the type of *C. umbrosa*, a fragment in the Engelmann Herb.), Nashville (Ward in 1877), Roan Mt. (Rydberg 8179, 8183). *Ohio;* Sandusky (York in 1902). *Indiana;* Blackford Co. (Deam 190, 512), Wilsons (Hill 100–1897), Vermilion Co.. (Deam 9817), Lake Co. (Hill 124–1897, 95–1876), Kosciusko Co. (Deam 444), Lagrange Co. (Deam 14856), Dune Park (Chase 522). *Michigan;* Port Huron (Dodge 104, 372, 4 collections without number in 1896), Detroit (Farwell 1291). *Illinois;* Without location (Chase), Evanston (Johnson in 1888), St. Clair Co. (Eggert in 1897, Brendel in 1880), Chicago (Scammon 1, Hill 120–1897), Wabash Co. (Schneck in 1880 and in 1881), west of Chicago. (Chase in 1894), Cook Co. (Chase in 1896), Joliet (Skeels & Shaddick in 1900), Riverside (Greenman 2782), Glencoe (Sherff in 1911), Athens (Hall 4), Highland (Meyer in 1841), Beardstown (Geyer in 1842), Mascoutah (Welch), Canton (Hovey); Peoria (Brendel), Carlinville (Andrews in 1890). *Wisconsin* (Hale in 1860–61). *Minnesota;* Fergus Falls (Sheldon in 1892), Cannon Falls (Pol in 1888). *S. Dakota;* Brookings (Williams in 1896), Lake Hendricks (Williams in 1894), Jones Island,

Big Stone Lake (Griffiths & Slosser in 1894), Watertown (Griffiths & Slosser 302). *Nebraska;* Bottoms of Yellowstone river (Hayden 26), Thomas Co. (Rydberg, two collections with number 1688, one collected August 26 and the other August 14, 1893), Holt Co. (Clements 2799), Ashland (Williams in 1889), Long Pine (Bates in 1896). *Missouri;* St. Louis Co. (Engelmann in 1860, 1842, 1843, August 1841 and Sept. 1841, taken as the type, in the Engelmann Herb., Eggert in 1879, Craig in 1908, Greenman 3800, Garber in 1911, Drushell in 1916), Barry Co. (Bush 202, 327, 3244, and without number in 1892), MacDonald Co. (Bush 28), Baring, (Bush 6), Polk Co. (Standley 9937), Courtney (Bush 411, 1815), Sarcoxie (Palmer 3197), Meramec (Pammel), Stone Co. (Trelease 1113), Seligman (Dewart in 1892), Anderson (Bush in 1892), Joplin (Palmer 3835). *Iowa;* Decatur Co. (Fitzpatrick 25). *Indian Territory;* Limestone Gap (Butler 19, 50, 94 and 11236?). *New Mexico* (Fendler 658) *Arizona;* Grand Canyon (Eggert in 1886). *Texas;* Williamson Co. (Bodin 230), Calvert (Pammel in 1888), Fort Smith (Ark.) to the Rio Grande (Bigelow 8). *Montana;* Popular (Blankinship in 1900).

Cuscuta indecora Choisy

C. indecora Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:278, pl. 3, fig. 3, 1841; and in DC., Prodromus, 9:457, 1845.—Matthew, Bull. Torr. Bot. Club, 20, pl. 164, fig. 4, 1893.—, Britton & Brown, Illustr. Flora, 3:29, fig. 2960, 1898; 2 ed., 3:50, fig. 3446, 1913.—Stevens, Amer. Journ. Bot., 3:185, figs. 3–4, 1916.

C. decora Engelmann, Trans. Acad. Sci. St. Louis, 1:501, 1859.

Epithymum indecorum (Choisy) Nieuwland & Lunell, Amer. Mid. Nat., 4:511, 1916.

Stems medium to coarse. Flowers 2–5 mm. long, whitish, fleshy, papillose to smoothish, on pedicels shorter or longer than the flowers, stigmas and anthers commonly purplish colored; calyx lobes triangular to lanceolate, acute or somewhat obtuse; corolla campanulate; lobes erect to spreading, triangular, acute, the tips inflexed; scales as long as or longer than the tube, ovate or somewhat spatulate or divided, deeply fringed, bridged at or below the middle; stamens shorter than the lobes; anthers broad, oval, about equal to the filaments; styles as long as or slightly longer than the globose, pointed ovary, unequal, becoming divaricate in fruit. Capsule globose, pointed, enveloped by the withered corolla; seeds about 1.7 mm. long, usually two to four in a capsule, roundish or broader than long, grayish or brown, somewhat scurfy; hilum small, oval, transverse or somewhat oblique.

While this species is quite variable it has been difficult to maintain varietal segregations. The majority of the collections fall under variety *neuropetala* which shows quite wide extremes of size, shape of parts, etc. It has been thought best to maintain a varietal segregation as indicated below although in many cases it is rather difficult to tell with exactness to which variety a form may belong.

Key to the varieties

Scales not divided, ovate or spatulate.
- Calyx lobes broad, ovate, acute.
  - Flowers about 2–3 mm. long, papillose-hispid ..... *hispidula*
  - Flowers usually larger, not so papillose-hispid ..... *neuropetala*
- Calyx lobes lanceolate, acute ..... *longisepala*

Scales divided at the apex ..... *bifida*

Cuscuta indecora hispidula (Engelmann) n. comb.

C. verrucosa hispidula Engelmann, Amer. Journ. Sci. & Arts, 43:341, 1842.
C. hispidula Engelmann, Amer. Journ. Sci. & Arts, 45:75, 1843.
C. neuropetala minor Engelmann, Bost. Journ. Nat. Hist., 5:223, 1847.
C. porphyrostigma, Engelmann, Bost. Journ. Nat. Hist., 5:223, 1847; in synon.
C. decora indecora Engelmann, Trans. Acad. Sci. St. Louis, 1:502, 1859.

Flowers 2–2.5 mm. long, usually on pedicels longer than the flowers; calyx mostly shorter than the corolla, more papillose-hispid than in the other varieties.

Type locality: "Mexicum ad Metamoros." Range: Texas, New Mexico and Indian Territory and in the Greater Antilles.

Specimens examined: (Berlandier 2285, the type number, in the Engelmann Herb. from Mexico?). UNITED STATES: *Texas;* (Berlandier 865, 965, Lindheimer 123, Nealley 141), eastern part of the state (Hall 491), Llano Co. (Nealley 83), Llano (Smith in 1897), New Braunfels (Lindheimer 318, 1029), San Antonio (Wilkinson in 1902), Fort Worth (Ruth 188), Columbia (Bush 1535), Fort Smith (Ruth 159), Dallas (Hall 493 in part). *New Mexico;* Fort Whipple (Coues & Palmer 246). *Oklahoma;* Greer Co. (Stevens 1000). *Indian Territory* (Sheldon 134).

WEST INDIES: *Cuba;* Camaguey (Shafer 2635). *Jamaica;* Port Antonio (Fredholm 3304).

Cuscuta indecora neuropetala (Choisy) Hitchcock
[Figures 44 a–e, 96 and 128]

C. indecora neuropetala Hitchcock, Contrib. U. S. Nat. Herb., 3:549, 1896.
C. neuropetala Engelmann, Amer. Journ. Sci. & Arts, 45:75, 1843.
C. neuropetala littoralis Engelmann, Bost. Journ. Nat. Hist., 5:223, 1847.
C. pulcherrima Scheele, Linnaea, 21:750, 1848.
C. decora pulcherrima Engelmann, Trans. Acad. Sci. St. Louis, 1:502, 1859.
?C. indecora portoricensis Urban, Symb. Ant., 4:502, 1910.

Flowers usually larger than in the other varieties, loose or compacted; corolla broadly campanulate, varying in its degree of papillation. Forms from the southeastern United States frequently are more waxy white than those from the west. The calyx lobes are shorter than or equalling the corolla.

Type locality: "Texas in wet prairies near Houston." Range: Illinois, westward to Utah and California, south into Mexico and through the southern states into the West Indies. The specimen reported from Michigan is believed to have been introduced with alfalfa seed from one of the western states.

Specimens examined: UNITED STATES: American plains (Hall & Harbour 464). *Michigan;* Shelby (Wagner in 1919). *Illinois* (Engelmann in 1845), St. Clair Co. (Eggert in 1877). *Minnesota;* Fergus Falls (Sheldon in 1892). *S. Dakota;* Washington Co. (Over 2157), Hot Springs (Petersen in 1908). *Nebraska;* Merrinem (Bates in 1896), Hooker Co. Mullen (Rydberg 1634, 1694), Waho (Rydberg), Banner Co. (Rydberg in 1890), Cheyenne Co. (Rydberg 3700). *Kansas;* Syracuse (Rose & Fitch 17027, Thompson 159). *Louisiana* (Langlois in 1879). *Mississippi;* Brush Island (Lloyd & Tracy 128), Cat Island (Lloyd & Tracy 124). *Alabama;* Mobile (Mohr in 1888, and in 1876, 885c). *Florida;* Santa Rosa Island (Tracy 6432), Wakulla Co., St. Marks (Harper 209), Colquitt Co. (Harper 1650),

Palma Sola Bay (Simpson 68), Tallahassee (Harper 224), Manatee (Simpson in 1889). *Colorado* (Herb. State. Agr. College 1541), Colorado Springs (Porter in 1873, Cooper 421), Evans (Johnson 399), Denver (Eastwood in 1890, 129), Fort Collins (Baker 555), Boulder (Daniels 426). *Texas* (Lindheimer 124, taken to represent the type, in the Engelmann Herb., 474, III 475), San Antonio (Nealley 94, Headly in 1907, Ball 919), Del Rio (Plank in 1891), Austin (Biltmore Herb. 3736a), Val Verde Co., Comstock (Nealley 126), Bexar Co. (Jermy 74, 75). *Arizona;* Globe (Goodding 724), Fort Lowell (Thornber 133), Pine (McDougal 685), Santa Cruz Valley (Pringle in 1884), Tucson (Thornber 32, 87, Smart 345, Griffiths 2155, Rose 11887, Pringle in 1884, Toumey 96), Rincon Mts. (Toumey in 1894), Santa Catalina Mts. (Pringle in 1881, Lemmon in 1881), Castle Creek (Toumey 293), Monmouth (Nealley 278). *New Mexico* (Wright 521, 525, 1622, 1630, 1632, 1633, 1634, 1638), Nara Visa (Fisher 147). *Utah;* Salt Lake City (Garrett 192, 1714, 1716, 1719, 2692, 2736, Jones 1331, in 1880). *Wyoming;* Laramie Co., Uva (Nelson 2741, in part, 8576), Sheridan Exp. Farm (Buffum 1405). *Idaho;* Moscow Exp. Station (Henderson 2892). *California* (Leiberg 5396), San Bernardino Co. (Parish 5532, 5905), Butte Co. (Brown 132, Heller 11677), Lake Co. (Bolander 2673, in part), Humboldt Co. (Chesnut & Drew in 1888), Clear Lake (without indication of collector), Clovis (Brandegee), Chico (Studley 4d), Fresno (Brandegee), Yolo Bolo Mt. (Brandegee in 1892), Shasta River, northern Calif. (Greene 978).

West Indies: *Cuba* (Wright 3649), Santa Clara (Britton, Britton & Wilson 5507). *Santa Domingo;* Barahona Province (Fuertes 117, 916, 975b). *Jamaica;* Port Antonio (Wight 73), Porto Rico (Sintensis 3851).

Mexico: *Sonora;* Hermosillo (Rose, Standley & Russell 12477). *Coahuila* (Purpus 4563), Parras (Purpus 6343). *Zacatecas* (Palmer 284). *San Luis Potosi;* San Dieguito (Palmer 630). *Tamaulipas;* Tampico (Palmer 530).

Cuscuta indecora longisepala n. var.
[Figures 44 f and 97]

Flowers subsessile, compacted; calyx lobes lanceolate, acuminate, as long as or exceeding the corolla. Some specimens approach variety *neuropetala* in their shorter calyx lobes.

Type locality: On the Blanco, Texas. Range: Indian Territory, Texas and northern Mexico.

Specimens examined: United States: *Texas;* on the Blanco (Wright, the type, in the Engelmann Herb.), Dallas (Reverchon in 1875, Hall 493, in part). *Indian Territory* (Butler 2), Limestone Gap (Butler in 1877).

Mexico: *Tamaulipas;* Tampico (Palmer 333). *San Luis Potosi;* San Dieguito (Palmer 640).

Cuscuta indecora bifida n. var.

Calyx lobes shorter than the very white corolla; scales rather deeply divided at the apex.

Type locality: Twin Springs, Nevada.

Specimens examined: United States: *Nevada;* Twin Springs (Purpus, the type, in the Univ. Calif. Herb.).

Cuscuta jepsonii n. sp.
[Figure 52]

Stems slender. Flowers 2–2½ mm. long, pentamerous, on pedicels shorter than the flowers, in cymose clusters, entire inflorescence fleshy and papillate; calyx lobes triangular, acute, scarcely reaching the middle

of the corolla tube; corolla globular, becoming urceolate, lobes upright or more or less connivent, triangular, acute, less than half as long as the corolla tube, not overlapping; scales represented only by ridges and short bridges; stamens much shorter than the corolla lobes; filaments about equal to the small, oval anthers; styles much shorter than the globose, slightly pointed ovary. Capsule depressed-globose, somewhat elevated about the intrastylar aperture, surrounded by the persistent corolla; seeds 2–4 in a capsule, rounded, compressed.

This species, which appears to be rare, differs greatly in many respects from *C. californica*, the only other North American species lacking infrastamineal scales. It differs from *C. sandwichiana*, a species not recorded from North America, which it resembles somewhat, in the fleshier texture of the whole plant, the size of the flowers and the shape of the corolla.

Type locality: Big Horse Mountain, South Fork of the Eel River, California.

Specimens examined: UNITED STATES: *California;* Big Horse Mountain, South Fork of the Eel River (Jepson 5c, the type, in the Univ. Calif. Herb.).

Cuscuta californica Choisy

C. californica Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:279, 1841;. and in DC., Prodromus, 9:457, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:498, 1859.

C. acuminata Nuttall in Engelmann, Trans. Acad. Sci. St. Louis, 1:498, 1859; nomen nudum, in synon.

Stems slender. Flowers 2–5 mm. long, glabrous or papillate, subsessile in compact clusters or on slender pedicels in loose panicled cymes; calyx as long as the corolla tube or shorter; lobes lanceolate, acute to acuminate, or shorter, ovate and somewhat obtuse, their tips frequently somewhat divergent; corolla campanulate or cylindrical; lobes ovate to lanceolate, acute or somewhat obtuse, as long as or longer than the tube, connivent to spreading or reflexed; scales rudimentary, represented only by short bridges or "inverted arches"; stamens shorter than the lobes; filaments shorter than or slightly longer than the oval to linear anthers; styles as long as or longer than the somewhat ovate or conic ovary. Capsule globose or ovoid-conic, enveloped by the withered corolla; seeds about 1 mm. long, oval, slightly compressed, rather rostrate, one to four in each capsule; hilum oblong, transverse or oblique.

Key to the varieties

Capsule globose, not pointed.
Flowers glabrous.
Anthers on definite filaments.
Calyx lobes acute to acuminate, usually reaching at least the middle of the corolla tube.
Flowers more or less pedicelled; styles as long as, or longer than the ovary ..... *graciliflora*
Flowers subsessile; styles shorter than the ovary ..... *breviflora*

Calyx lobes rather obtuse, not reaching the middle of the corolla tube..... ..... *brachycalyx*
Anthers sessile or subsessile..... *apodanthera*
Flowers papillose..... *papillosa*
Capsule ovoid-conic..... *apiculata*

Cuscuta californica graciliflora Engelmann
[Figures 45 a–c, 74, 84 and 151]

C. californica graciliflora Engelmann, Trans. Acad. Sci. St. Louis, 1:499, 1859.
C. californica longiloba Engelmann, Trans. Acad. Sci. St. Louis, 1:499, 1859.

Flowers rather variable in size, somewhat pedicelled; calyx lobes ovate; corolla cylindrical to campanulate; lobes connivent to reflexed; anthers elliptical to oblong; styles as long as or longer than the ovary.

I have been unable to keep apart the two varieties indicated by Engelmann. The specimens included here are usually called variety *longiloba* in collections.

Type locality: "Nov. Californiam." Type not seen. Range: Pacific coast states from Washington to Lower California.

Specimens examined: UNITED STATES: *California* (Orcutt in 1888, Collins & Kempton 315, Leiberg 5267), San Benito Island (Anthony 266), Amador (Michener & Bioletti in 1893), San Felipe (Thurber 633), San Diego Co. (Anderson in 1894, Chandler 5199), San Diego (Thurber 570, Wooton in 1903, Parry in 1850, Orcutt 1499), Surf (Brandegee), Santa Clara Co. (Brewer 1283), Pacheco's Pass (Brewer 1292, in part), Claremont (Chandler in 1897), Escondido (Chandler 5384), Los Angeles Co. (Abrams 1560, 2654), Los Angeles (Tracy in 1888), Azuza (Baker 1560), Brush Canyon near Cahuenga Peak (Chandler 2010), Napa Co. (Jepson 70c), Santa Lucia Mts. (Jepson 1704), Riverside (Hall in 1897, Brandegee in 1905), Yosemite National Park (Hall 9219), Rubio Canyon (Peirson 150a), Ramona (Brandegee in 1905), Badger (Brandegee in 1892), Sierra Nevada Mts. (Lemmon in 1875), San Bernardino Co. (McGregor & Abrams 700), San Bernardino (Coville & Funston 102), Mendocino Co. (McMurphy 55), Ventura Co. (McGregor & Abrams 36), Cleveland National Forest (Hitchcock in 1915), Julian (Hitchcock), San Francisco Co. (Michener & Bioletti in 1891), San Clemente Island (Trask 187), Lake Tahoe (Leiberg 5330), Coloma (Palmer 2392d), Tulare (Palmer 2761), Death Valley (Coville & Funston 338), Monsovia (Rubsy in 1909). The following four specimens are somewhat larger than normal. Black Rock Mts. (Leiberg 5266, labelled *C. newberryi*), San Antonio Mts. (Hall), Kern Co. (Burtt-Davy 1941). *Washington;* Spokane (Turesson in 1913).

MEXICO: *Lower California* (Brandegee 7), San Fernando (Brandegee in 1889).

Cuscuta californica breviflora Engelmann
[Figures 45d and 77]

C. californica breviflora Engelmann, Trans. Acad. Sci. St. Louis, 1:499, 1859.

Flowers subsessile in dense glomerules; corolla somewhat narrowly campanulate; stamens and styles short; anthers oval. The flowers as the capsule matures, when viewed from above, present a rather characteristic stellate appearance because of the spreading of the lobes.

Type locality: Monterey, California. Type not seen. Range: Pacific coast states, and inland to western Colorado:

Specimens examined: UNITED STATES: *Oregon;* La Grande (Cusick 2347), Grant's Pass (Howell in 1884), Wallowa Co. (Sheldon 8715), Cougar Peak (Coville & Leiberg 175).

Washington; Peshastin (Sandberg & Leiberg 495), Blue Mts., southeastern part of the state (Horner 373). *California;* San Francisco (Gardner in 1901), Monterey Co. (Chandler 423), San Benito Island (Brandegee in 1897), Siskiyou (Butler 15), Santa Catalina Island (Brandegee in 1890), Humboldt Co. (Tracy 4760), Mt. Silliman (Brandegee in 1905), Yosemite Valley (Hall 9094), Contra Costa Co. (Elmer 4543), Tuolumne Valley (Bolander 5055), Clear Lake (Torrey 325). *Nevada;* Rhyolite (Heller 9684). *Utah;* Bingham (Jones 1875), Jordan Valley (Watson 938), City Creek Canyon (Jones 1915), Salt Lake Co. (Garrett 2170). *Colorado;* Paonia (Osterhout 4602).

MEXICO: *Lower California;* San Bartolomé Bay (Rose 16206).

Cuscuta californica brachycalyx n. var.

[Figures 45 e–f and 75]

Flowers in dense cymose clusters; calyx very short; lobes broadly ovate, obtuse to acutish; corolla campanulate; lobes reflexed, shorter than the tube, triangular, acutish.

Type locality: Near Hanford, California. Range: Found so far only in California.

Specimens examined: UNITED STATES: *California;* Near Hanford (Kearney 52, the type, in the N. Y. Bot. Gard. Herb.), Fresno (Sones 79), Yosemite Valley, Stoneman Bridge (Reed in 1911), Dugan (Brandegee in 1914), Vacaville (Jepson in 1891), Clear Lake mountain region (Jepson 5b), Solano Co. (Jepson 5d), Snow Mt. (Brandegee), Tulare Co. (Michener & Bioletti in 1893), Goshen (Congdon 66), Tulare (Congdon 65).

Cuscuta californica apodanthera n. var.

Corolla campanulate; calyx lobes short, acute, arising from a fleshy flower base which tapers into the pedicel; anthers sessile or subsessile on very short filaments.

Type locality: Yosemite Valley, California.

Specimens examined: UNITED STATES: *California;* Yosemite Valley (Jepson 80a, the type, in the Univ. Calif. Herb.), Potter Valley (Jepson 125a).

Cuscuta californica papillosa n. var.

[Figure 76]

Flowers in loose or compact clusters, papillose pubescent.

Type locality: San Bernardino Valley, California. Range: Found so far only in California.

Specimens examined: UNITED STATES: *California;* San Bernardino Valley (Parish 5524, the type, in the Rocky Mt. Herb. in Univ. Wyo.), San Jacinto Mts. (Hasse in 1892, Hall in 1901), Riverside Co. (Parish 4130), Riverside (Reed 2372), Santa Lucia Mts. (Jepson 1628), Monterey Co. (Vasey 437), San Diego Co. (Parish 538a), Lake Co., Elk Mt. (Tracy 2349).

Cuscuta californica apiculata Engelmann

[Figure 45 g]

C. californica apiculata Engelmann, Trans. Acad. Sci. St. Louis, 1:499, 1859.

Corolla somewhat granulate, particularly towards the base, campanulate; ovary and capsule ovoid, pointed.

Only one specimen, the type, was seen. The pointed capsule is definite and warrants the segregation of the plant as a variety.

Type locality: "On the Colorado," California.

Specimens examined: UNITED STATES: *California;* On the Colorado (Bigelow in 1854, the type, in the Engelmann Herb.).

Cuscuta harperi Small
[Figures 21, 123 and 134]

C. harperi Small, Flora of the Southeastern United States, (2 ed.), p. 1361, 1913.

Stems very slender. Flowers penta-, tetra- or trimerous, about 1 mm. long, on pedicels mostly as long as or longer than the flowers in loose racemose clusters; calyx shallow, the lobes short, broadly ovate, obtuse. frequently slightly keeled and tuberculate; corolla campanulate; lobes triangular-ovate, acute, about equalling the tube, upright, slightly fleshy, with their tips inflexed, in fruit upright or reflexed; scales narrow, fringed with a few short processes particularly about the upper half, as long as or somewhat longer than the corolla tube, bridged at about one-third their height; stamens shorter than the lobes, filaments slightly tapering and equal to the small, oval anthers; ovary globose-oval, with a slightly thickened collar about the intrastylar aperture; styles slender, shorter than the ovary; stigmas capitate. Capsule oval, with the withered corolla at its base; seeds about 1–1.2 mm. long, ordinarily but one in a capsule, yellow brown, somewhat spherical; hilum a fine line, transverse or oblique, the umbilical area somewhat sunken.

This species seems to be rather rare. It closely resembles some of the smaller specimens of *C. pentagona typica*, from which it differs in the shape of its scales, calyx and capsule.

Type locality: Etowah Co., Alabama. Range: Northern Alabama.

Specimens examined: UNITED STATES: *Alabama;* Etowah Co. (Harper 147, taken as the type, in the N. Y. Bot. Gard. Herb., Pollard & Maxon 341), De Soto Falls (Ruth 493, and in 1893).

Cuscuta rostrata Shuttleworth
[Figures 40, 102, 103 and 139]

C. rostrata Shuttleworth in Engelmann, Bost. Journ. Nat. Hist., 5:225, 1847.—Engelmann, Trans. Acad. Sci. St. Louis, 1:508, 1859.—Matthew, Bull. Torr. Bot. Club, 20, pl. 165, fig. 10, 1893.—Britton & Brown, Illustr. Flora, 3:30, fig. 2964, 1898; 2 ed., 3:51, fig. 3450, 1913.

C. oxycarpa Engelmann, Bost. Journ. Nat. Hist., 5:225, 1847; in synon.

Stems coarse. Flowers glabrous, 4–6 mm. long, pentamerous, on pedicels shorter than the flowers in compact, paniculate cymes; calyx shorter than the campanulate corolla; lobes ovate, obtuse, overlapping; corolla membranaceous, cells very evident, somewhat thickened lines running lengthwise below the stamen insertions giving the corolla a rather angled appearance; lobes shorter than the tube, broad, ovate, obtuse, erect, becoming spreading and later reflexed in fruit; scales shorter than the tube, oblong, deeply fringed with long processes, shorter processes frequently evident on the bridge which is about a third of their height;

stamens shorter than or about as long as the lobes; anthers oval, shorter than the subulate filaments; ovary flask-shaped with a long somewhat two-beaked neck; styles shorter than the ovary. Capsule globose, flask-shaped, beaked, enveloped by the withered corolla; seeds light brown, about 2.4 mm. long, varying from one to four in each capsule, slightly rostrate, obovate or oblong, oblique; hilum oblique or transverse, the umbilical area slightly striated.

Type locality: Little Craggy Mountains, N. Carolina. Range: In the Alleghany Mountains from Virginia to South Carolina.

Specimens examined: United States: *W. Virginia* (Gray & Sullivant in 1853), White Sulphur Springs (Steele in 1906). *N. Carolina* (Rugel, without number or date, perhaps the same as the type collection, Curtis in 1845, Canby in 1880, Ashe), Waynesville (Stanley 5372, Canby in 1876), Balsam Mts. (Ball in 1890, Canby in 1876), Mt. Mitchell (Biltmore Herb. 5727), Transylvania Co. (Biltmore Herb. 5727a), Buncombe Co. (Biltmore Herb. 5727b), Roan Mt. (Canby in 1884, Chickering in 1877 and in 1880, Cannon 172, Ashe), Biltmore (Mohr in 1899), Little Craggy Mts. (Rugel in 1841, the type, in the Engelmann Herb.), Grandfather Mt. to Linville (Hitchcock in 1905), Swain Co. (Beardsley & Kofoid in 1891). *S. Carolina* (Buckley in 1842). *Tennessee;* Cocke Co. (Kearney 842), Gattingsberg (Canby in 1888).

Cuscuta gronovii Willdenow

C. gronovii Willdenow in Roemer & Schultes Syst., 6:205, 1820.—Choisy Mém. Soc. Phys. et Hist. Nat. Genève, 9:281, pl. 4, fig. 3, 1841; and in DC., Prodromus, 9:459, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:507, 1859.—Matthew, Bull. Torr. Bot. Club, 20, pl. 165, fig. 9, 1893.—Britton & Brown, Illustr. Flora, 3:30, fig. 2963, 1898; 2 ed., 3:51, fig. 3449, 1913.—Stevens, Amer. Journ. Bot., 3:185, figs. 7–8, 1916.

Epithymum gronovii (Willdenow) Nieuwland & Lunell, Amer. Mid. Nat., 4:511, 1916.

Stems medium to coarse. Flowers glabrous, about 2–4 mm. long, pentamerous, on pedicels as long as or longer than the flowers, in loose or dense panicled cymes; calyx lobes broad, ovate, orbicular or oblong, obtuse, overlapping, shorter than or equalling the corolla tube, sometimes somewhat serrated; corolla campanulate, its lobes as long as or shorter than the tube, obtuse, spreading; scales variable, shorter than the tube or equalling it, ovate or oblong, infrequently more or less truncated or divided, deeply fringed with longer processes towards the apex and shorter ones towards the base and frequently on the bridge which is below the middle; stamens nearly as long as the lobes; filaments longer than the oval anthers; styles shorter than the globose, conical ovary. Capsule globose-conic, umbonate, enveloped by the corolla or infrequently bearing this about its apex; seeds about 1.5 mm. long, two to four in a capsule, compressed, obliquely ovate, slightly rostrate, brown; hilum linear, oblique or transverse.

The specimens of this species show great variation in the size of flowers and shape of parts.

Key to the varieties

Corolla ordinarily surrounding (not capping) the capsule.
- Calyx lobes about as long as the shallowly campanulate corolla ..... *latiflora*
- Calyx lobes usually shorter than the more cylindrical corolla ..... *vulgivaga*

Corolla capping the capsule ..... *calyptrata*

Cuscuta gronovii latiflora Engelmann
[Figure 37 f–g]

C. gronovii latiflora Engelmann, Trans. Acad. Sci. St. Louis, 1:508, 1859.
C. saururi Engelmann, Amer. Journ. Sci. & Arts, 43:339, pl. 6, figs. 17–21, 1842.
C. gronovii saururi MacMillan, Geol. & Nat. Hist. Surv. of Minn. I. The Metaspermae of the Minnesota Valley, p. 430, 1892.

Calyx lobes nearly as long as or equalling the shallowly campanulate corolla, the lobes of which equal the tube.

Type location: "In the 'American Bottom' opposite St. Louis." Range: New Jersey and westward to Missouri and southward to Texas.

Specimens examined: UNITED STATES: *New Jersey;* New Brunswick (Vail in 1890), Spotswood (Taylor 2606). *Pennsylvania;* Harrisburg (Porter in 1879), York Co. (without indication of collector). *Illinois;* Opposite St. Louis (Geyer in 1841, taken as the type, in the Engelmann Herb., Engelmann in 1843, Eggert in 1877). *Missouri* (Short in 1843), St. Louis (Engelmann in 1841, in 1845, Riehl in 1843), Butler Co. (Russell), Clay Co. (Mackenzie 370), Webb City (Palmer 2737), Jasper Co. (Palmer 1292). *Indian Territory;* Cherokee Nation (Blankinship in 1895). *Texas;* Dallas (Reverchon).

Cuscuta gronovii vulgivaga Engelmann
[Figures 37 a-e, 100, 101 and 148]

C. gronovii vulgivaga Engelmann, Trans. Acad. Sci. St. Louis, 1:508, 1859.
C. vulgivaga Engelmann, Amer. Journ. Sci. & Arts, 43:338, pl. 6, figs. 12–16, 1842.
C. americana of various authors, according to Engelmann, Trans. Acad. Sci. St. Louis, 1:508, 1859; in synon.
C. polyantha Shuttleworth in Engelmann, Trans. Acad. Sci. St. Louis, 1:508, 1859; in synon.
C. umbrosa Beyrich in Engelmann, Trans. Acad. Sci. St. Louis, 1:508, 1859; in synon.

Corolla deeper, less openly campanulate than in variety latiflora, its lobes ordinarily shorter than the tube; calyx lobes usually not reaching the sinuses. The commonest of the varieties.

C. vulgivaga of Engelmann when published was made to consist of three nominal varieties though he did not keep up this segregation later. These were variety *laxiflora* which may have been considered most representative of the species and which included most of the material from the interior of the country, and the type of which seems to have been a specimen collected in New York state by Dr. Gray; variety *glomerata* from Vermont, collected by Carey and variety *tetramera* from Connecticut, collected by Carey.

Type locality: "Western New York." Type not seen. Range: From Canada to Florida and westward to Nebraska, Arizona and Texas.

Specimens examined: UNITED STATES: *Maine* (Ricker 469), Aroostook Co. (Fernald 88), Veazie (Knight in 1905), Maxfield (Ricker 1396, 1397), Auburn (Merrill 699), Machiasport (Barber in 1898), Leeds (Sturtevant in 1862), Orono (Harvey & Harvey 699 and in 1895), Cape Elizabeth (Gayle 811). *Massachusetts;* Belmont (Pound in 1889), Andover (Foster in 1901), Littleton (Harwood in 1901), Williamstown (without name of collector, Day 64), So. Hadley (Cook in 1887), Northampton (Stevens in 1895), Morrison (Morris in 1897), Cambridge (Engelmann in 1856), Nonquit (Sturtevant in 1888), Lincoln (Greenman 2138), Amherst (Woolson 17194), Hampden Co. (Seymour 20), Riverside (Greenman 1478). *Rhode Island;* Cumberland (Greenman 1825). *Connecticut;* Cromwell (Brandegee in 1869),

Bridgeport (Eames in 1894). *New Hampshire* (Carey). *Vermont;* Brandon (Knowlton in 1895), Wallingford (Banker 556). *Maryland;* Chesapeake Bay (Shull 112, 189, 289, 368), Elkton (Shreve 381), Cabin John (Chase 2626). *District of Columbia;* Washington (Steele in 1912, Tweedy in 1890 , Oldberg in 1872, Ward in 1876, Hitchcock in 1904). *West Virginia;* Greenbriar Co. (Steele in 1906), Aurora (Steele in 1898), Jefferson Co. (Palmer 22), Upshur Co., Bucklin (Pollock). *Virginia;* Luray (Steele 93), Marion (Rydberg 8073). *New Jersey;* Passaic Co. (Mackenzie 3797), Camden (Martindale). *N. Carolina;* (Chalmot, Curtis in 1845, Buckley in 1844), Plymouth (Hemmick 4), Biltmore (Biltmore Herb. 2126a), Polk Co. (Townsend in 1897), Stanley Co., Falls of Yadkin River (Small in 1894), Ashville (Gray & Sullivant in 1843), Hillsborough (Curtis). *S. Carolina;* Oconee Co. (Anderson 1385), Big Stone (Williams in 1892). *Florida;* Lee Co. (Hitchcock 232), Ft. Meyer (Simpson 380). *Alabama* (Buckley in 1841, Shuttleworth in 1843), Mobile (Mohr in 1872, in 1882, in 1893 and in 1896), Marshall Co. (Milligan in 1907), Franklin Co. (Prout in 1840). *Georgia;* (Carey), Rome (Without name of collector, in 1891). *Louisiana;* New Orleans (Cocks), Natchitoches (Palmer 8710). *Tennessee;* Nashville (Gattinger in 1886), Knoxville (Bain in 1894), Chattanoga (Engelmann in 1876), Hiawassee Valley (Ruth 8), Jackson (Bain 338). *Kentucky* (Short in 1840), Bell Co. (Kearney 472, 588). *New York;* Oneida Co. (Maxon in 1897), West Chester Co. (Pollard in 1894), Oxford (Coville in 1895), Dutchess Co. (Standley & Bullman 12271), New Lebanon (Harrison in 1888), Round Lake (McCall in 1877), Coeman Hollow (Shear in 1891), Fort Ann (Burnham 37), LeRoy (Hill 151–1871), Honeoye Lake (Hill 81–1884), Buffalo (Clinton in 1864), Tarrytown (Schrenk in 1892), Oswego Co., South Scriba (Rowlee in 1906). *Pennsylvania;* Meadville (Clinton), Easton (Porter in 1869), Buck Co. (Mayer in 1867), Penn Yan (Bartwell), Millersville (Small in 1890), York Co. (Heller & Halbach 1357), Sellersville (Fretz in 1882), Reading (Bischoff in 1848), Lower Merron (Redfield 5853), Fairmont Park (Redfield 5854), Chester Co. (Canby 3), Bethlehem (Moser 1832), Montgomery Co. (Brinton in 1888), Philadelphia (Greenman 1477), Pocono Plateau (Harshberger in 1904). *Ohio;* Oxford (Fink 305), Berea (Ashcraft in 1895), Albion (Ashcraft in 1895), Granville (Jones 1370), Elyria (Dick in 1890 and in 1895), Painesville (Beardslee in 1876). *Michigan;* Flint (Clark 4264), Lansing (without name of collector, in 1885), Cass Co. (Pepoon 190, 191, 450), Rochester (Brotherton in 1898), Greenville (Barlow in 1900), Macomb Co. (Cooley in 1882), Alma (Davis in 1889 and in 1892), Van Buren Co. (Pepoon 837, 892), Berrien Co. (Lansing 3301), Haslett (Yuncker 742), Portland (Yuncker 695). *Indiana;* Steuben Co. (Deam in 1904, 1906), Indianapolis (Yuncker in 1916), Putnam Co. (McDougal in 1889), Muncie (Brady in 1896), Notre Dame (Nieuwland 11500), Olio (Wilson in 1897), Adams Co. (Deam 5364 in part), Whitley Co. (Deam 21696, in 1897), Clark Co. (Deam 5473, 7600, 23800), Brown Co. (Deam 12225), Jefferson Co. (Deam 18784), Noble Co. (Deam 14701), Lagrange Co. (Deam 14888), Hamilton Co. (Deam 12129), Decatur Co. (Deam 9535), Carroll Co. (Deam 15339), Jackson Co. (Deam 30240), Dubois Co. (Deam 28267), Vigo Co. (Deam 24014), Knox Co. (Deam 26575), St. Joseph Co. (Deam 26391), Harrison Co. (Deam 26831), Wayne Co. (Deam 23860), Porter Co. (Deam 29812), Posey Co. (Deam 22339), Franklin Co. (Deam in 1903). *Illinois;* St. Clair Co. (Eggert in 1891), Chicago (Moffatt 1650=525), Gardner's Park (Chase 600), South Chicago (Hill 134–1882), Mt. Carmel (Schneck), Palmyra (Schneck), Stark Co, (Chase 169, and in 1896), Canton (Hovey),Elgin (Sherff 1813, 1979), Peoria Co. (Chase 1181). Peoria (McDonald in 1886 and in 1887), Beardstown (Geyer in 1842), Bluff Lake (Pammel in 1886), Athens (Hall in 1860), Joliet (Greenman 2695). *Wisconsin;* Milwaukee (Lapham in 1842, Hasse in 1882), Madison (without indication of collector, in 1893), Fulton (Hall 2). *Minnesota;* Little Lake (Taylor in 1892), Aiken Co. (Sandberg 841), Wabasha Co. (Scott in 1886), Clitherall (Campbell in 1897), Winona (Holzinger in 1888), Minneapolis (Sandberg in 1890). *S. Dakota* (Duffey in 1889, Griffiths & Slosser 38, 105). *Missouri* (Bush in 1888), Butler Co. (Eggert in 1893), Monteer (Bush 215, 4909, 7868), Green Co. (Standley 9502),

Turner (Standley 9848), Sibley (Bush 812), Fish Lake (Bush in 1888), St. Louis (Eggert in 1878), Polk Co. (Standley 9902), Jackson Co. (Bush 1011, 1067), Barry Co. (Trelease 1112), McDonald Co. (Palmer 4149), Meramec (Pammel in 1886), Bismark (Bush in 1893), Campbell (Bush in 1893), Taney Co. (Eggleston 12249), Jasper Co. (Palmer 808, 2737, 2821). *Nebraska;* Holt Co. (Clements 2799½), Lincoln (without indication of collector in 1889). *Arizona;* Grand Canyon (Eggert in 1886). *Texas;* Columbia (Bush 1509, 1568, 1569). *Arkansas;* Prescott (Hollister 120), Little Rock (without name of collector, in 1885), Baxter Co. (Palmer 4757), Marion Co. (Palmer 8407). *Indian Territory* (Bush 387), Cherokee Nation (Blankinship in 1895), Sapulpa (Bush 1416).

CANADA: (Armstrong in 1892). *Ontario;* Kingston (Fowler in 1884 and in 1894). *New Brunswick;* Miramichi, Black River (Fowler in 1892), Fredricton (Fowler in 1880). *Quebec;* Longueuil (Brother Victorin 3147).

Cuscuta gronovii calyptrata Engelmann

C. gronovii calyptrata Engelmann, Trans. Acad. Sci. St. Louis, 1:508, 1859.
C. calyptrata (Engelmann) Small, Flora of the Southeastern United States, p. 969, 1903.
C. bonariensis Engelmann, Trans. Acad. Sci. St. Louis, 1:508, 1859; in synon.

Flowers deeper campanulate and relatively larger; corolla surrounding the apex of the capsule. The specimens of *C. bonariensis* in Engelmann's herbarium are definitely characterized by the corolla capping the capsule, but it is somewhat doubtful to the writer if the specimens of *C. gronovii* exhibiting this character less definitely are the same.

Type locality: Western Louisiana. Range: Texas to Louisiana.

Specimens examined: UNITED STATES: *Louisiana* (Gregg, taken as the type, in the Engelmann Herb.). *Texas;* Houston (Lindheimer in 1841, 235?).

Cuscuta curta (Engelmann) Rydberg
[Figures 38, 98, 99 and 136]

C. curta (Engelmann) Rydberg, Bull. Torr. Bot. Club, 40:466, 1913.—Stevens, Amer. Journ. Bot., 3:185, figs. 5–6, 1916; (not *C. plattensis*).
C. umbrosa Hooker, Fl. Bor. Amer., 2:78, 1840; (in part) according to Engelmann, Trans. Acad. Sci. St. Louis, 1:508, 1859.
C. gronovii curta Engelmann, Trans. Acad. Sci. St. Louis, 1:508, 1859.
C. megalocarpa Rydberg, Bull. Torr. Bot. Club, 28:501, 1901.

Stems coarse. Flowers glabrous, about 2–3 mm. long, pentamerous, on short pedicels as long as or sometimes shorter than the flowers, in cymose panicles, the clusters becoming globular because of the growth and crowding of the capsules; calyx lobes ovate, obtuse, overlapping, their edges infrequently slightly serrulate and uneven, reaching about the middle of the corolla; corolla campanulate; lobes triangular, obtuse, spreading ordinarily reflexed in fruit, scales shorter than the tube, rather variable, but mostly truncated or more or less divided and fringed with medium length processes, bridged at about the middle; stamens slightly shorter than or about as long as the corolla lobes; anthers oval, about equal to or shorter than the subulate filaments; ovary globose-conic, styles very short, about one-fourth the length of the ovary. Capsule globose-conic, somewhat umbonate or beaked, 3–6 mm. in diameter, with the withered corolla

mostly about the upper part but sometimes at the base; intrastylar aperture rather large; styles usually convergent; seeds about 2–2.8 mm. long, slightly rostrate; hilum transverse or oblique.

This species is closely allied to *C. gronovii*. It differs from it, however, in the possession of a much larger capsule, shorter styles, and usually bifid and truncated scales.

Type locality: "Northwestern America." Range: Minnesota to Wyoming and south to Colorado and New Mexico.

Specimens examined: UNITED STATES: Southwest Kansas to New Mexico (Bell in 1867), Northwest America (Fremont's 3rd Exped. 79, the type, in the Engelmann Herb.). *Minnesota;* Chatfield (Hall 3), Preston (Hill 66–1876, Leach in 1861). *N. Dakota;* Benson (Lunell in 1909, 1912), Leeds (Lunell in 1907), Walhalla (Waldron 1697), Valley City (Perrine in 1896), Ward Co. (Lunell in 1908), Dunseith (Lunell in 1907). *S. Dakota;* Black Hills (Petersen in 1909). *Nebraska;* Ashland (Williams 355). *Colorado;* Huerfano Co. (Greene in 1913), Canyon City (Brandegee 704), Platte Canyon, Dome Rock (Jones 571), La Veta (Vreeland 670, the type of *C. megalocarpa*, in the N. Y. Bot. Gard. Herb.), Colorado Springs (Porter in 1873), Ute Pass (Porter in 1873), Manitou (without indication of collector, in 1885, Mulford in 1892). *Wyoming;* Horseshoe Park (Nelson 5053), Plumbaga Canyon (Schueburt in 1893). *Utah* (Tracy in 1887), Salt Lake City (Jones in 1880), City Greek Canyon (Jones 1914, Leonard 250 and in 1883). *Montana;* Belt River (Williams 220). *New Mexico;* Lincoln Co. (Wooton & Standley 3488, 3959), Balsam Park (Ellis 221, 224).

Cuscuta denticulata Engelmann
[Figures 46, 83 and 146]

C. denticulata Engelmann, Amer. Nat. 9:348, 1875.—Hillman, Nev. Agr. Exp. Sta. Bull., No. 15, fig. 5, 1892.

Stems very slender. Flowers glabrous, about 2 mm. long, pentamerous subtended by one to three denticulate, ovate-lanceolate, acute bracts, one to several in scattered glomerules; calyx lobes orbicular, obtuse, denticulate, deeply divided, overlapping, enclosing the corolla tube; corolla campanulate, becoming urceolate in fruit; lobes ovate, oval or slightly oblong, somewhat overlapping, about equalling the tube, spreading to reflexed; scales denticulate, about reaching the anthers, oblong-ovate, bridged at about the middle; anthers oval, shorter than the corolla lobes; about equalling the filaments; styles shorter than the small conic ovary; stigmas small. Capsule globose, conic, bearing the withered corolla at the apex, mostly one- or infrequently two-seeded; seed about 1 mm. long, light brown, globose-ovoid; hilum small. The embryo is thickened into a large round knob at the plumule? end.

Type locality: St. George, Utah. Range: Southern Utah, Nevada and California.

Specimens examined: UNITED STATES: *Utah;* St. George (Parry 205, the type, in the Engelmann Herb.). *Nevada;* Esmeralda Co. (Schockley 443), Reno (Curran in 1888, Hillman in 1891), Pyramid Lake (Curran in 1883, without indication of collector, in 1883). *California;* The Needles (Jones in 1884, Rose 12074), San Bernardino Mts. (Parish 3230, 3231, 3236), Mojave Desert, Tehachapi Pass (Abrams & McGregor 505), Palmdale (Abrams & McGregor 522), San Diego Co. (Orcutt in 1898), Barstow (Brandegee in 1909), San Bernardino Co. (Parish 2436).

Cuscuta veatchii Brandegee

C. veatchii Brandegee, Proc. Calif. Acad. Sci., II, 2:189, 1889.

Stems medium to slender. Flowers glabrous, about 2 mm. long, pentamerous, on pedicels shorter than the flowers, single or in clusters of two to five, forming small lateral umbels; calyx membranous, longer than the corolla tube; lobes ovate-deltoid, overlapping, acute, denticulate; corolla campanulate; lobes ovate and acute to lanceolate and acuminate, edges denticulate, as long as the tube, slightly overlapping, spreading; scales thin, rather difficult to study, reaching the filaments or infrequently shorter, fringed with medium length processes, bridged at about the middle; stamens on filaments shorter than or equalling the oval anthers; styles about as long as the globose-ovoid ovary; stigmas capitate. Capsule globose-ovoid, carrying the withered corolla at the apex; seeds, usually but one in each capsule, roundish, light brown, pitted(?); hilum terminal. The embryo is enlarged at the plumule (?) end into a large round knob, as in *C. denticulata*.

This species is in many respects similar to *C. denticulata*, but differs in its more deltoid calyx lobes and in the flowers being somewhat pedicellate. (Rare and exceptional specimens of *C. denticulata* are also somewhat pedicellate.)

Cuscuta veatchii typica

[Figures 48 a–e and 60]

Corolla lobes deltoid-ovate, acute; anthers oval, on short filaments; scales ordinarily about reaching the filaments.

Type locality: Ubi, Lower California. Range: From southern California to Lower California.

Specimens examined: UNITED STATES: *California;* The Needles (Jones 3862), San Diego Co. (Orcutt).

MEXICO: *Lower California;* Santa Maria (Brandegee in 1889), Ubi (Brandegee in 1889, the type, in Univ. Calif. Herb. as sheet 105,066), San Roquis (Brandegee in 1889).

Cuscuta veatchii apoda n. var.

[Figure 48 f]

Corolla lobes lanceolate, acute to acuminate, slightly longer than the tube; scales shorter than the tube; anthers oval-oblong, sessile.

Type locality: Las Vegas, Nevada. Range: Nevada.

Specimens examined: UNITED STATES: *Nevada;* Las Vegas (Goodding 2296, Wooton in 1916, the type, in the U. S. Nat. Herb. as sheet 768,922, Brandegee in 1915), Sodaville (Brandegee in 1913).

Cuscuta subinclusa Durand & Hilgard

[Figures 47, 73 and 147]

C. subinclusa Durand & Hilgard, Journ. Acad. Nat. Sci. Phil., II, 3:42, 1855.—Engelmann, Trans. Acad. Sci. St. Louis, 1:500, 1859.

?C. ceanothi Behr, Proc. Calif. Acad. Nat. Sci., 1:17, .854.

Stems medium, somewhat fleshy in some specimens. Flowers about 5–6 mm. long, pentamerous, sessile or on pedicels shorter than the flowers in few to several flowered clusters which may be either scattered or approximated into dense, continuous masses; calyx not reaching, or surpassing the middle of the corolla tube; lobes broadly ovate to lanceolate, acute, sometimes cuspidate, overlapping, somewhat loose about the corolla; corolla cylindrical, usually showing cross wrinkles or striations, slightly fleshy, the cells somewhat lens shaped causing the edges of the lobes to be crenulate; lobes slightly overlapping, ovate, acute, erect to spreading, much shorter than the tube; scales oblong, about half as long as the tube, fringed with short processes, bridged at about one-third of their height; anthers oblong, subsessile to sessile; styles slender, much longer than the subglobose ovary; stigmas capitate. Capsule oval, pointed, thickened in the form of a collar about the intrastylar aperture, capped by the withered corolla; seeds about 1.8 mm. long, usually but one in each capsule, globose, slightly compressed, yellow brown; hilum situated at the broader end in a depression, short, oblong, oblique.

Type location: Tejon Pass, California. Type not seen. Range: Pacific coast states, from Oregon to Mexico.

Specimens examined: UNITED STATES: Valley of Palms (Jones 3712). *California* (Bolander 2698, 2849, 6381, Lemmon in 1878, Brewer 1292, in part, Bridges, Bioletti in 1892, Wright in 1853–56, Rattan 293, Newberry), Mt. Tamalpais (Jepson in 1892, Chesnut in 1887), Cuyamaca (Hitchcock in 1915), Vacaville (Jepson 3b; 3c); Napa Mts. (Jepson 4a), Santa Cruz Mts. (Hitchcock 205), Sequoia Nat. Park (Copeland 73), Owen's Valley (Horn in 1863, 2849), Claremont (Baker 3954), Calaveras Co. (Hansen 1275), San Bernardino Co. (Pringle 145), San Bernardino Valley (Parish 5533), San Bernardino (Parish 539, 3958), Napa Co. (Chandler 7123), Napa River Basin (Jepson, 1735, 7124), Nevada Co. (Jones 2490), Lake Co. (Bolander 2674), Los Angeles Co. (Brewer 68), St. Helena (Jepson 70a; 70b), Niles (Jepson 125b), Sherman (Braunton in 1902), Redondo (Braunton in 1902), Los Angeles (Hasse in 1890), Santa Clara Co. (Baker 57), Sierra Co. (Brewer 2698), Quincy (Eggleston 7649), Lassen's Peak (Austin 492), Rubio Canyon (Peirson 150), Contra Costa Co. (Bolander 2436), Modoc Co. (Manning 497, 498), Lathrop (Bioletti in 1892), San Joaquin River Bridge (Brandegee in 1892), Ramona (Brandegee in 1894), Mt. Wilson (Peirson 261), Tulare Co. (Engelmann in 1880, Congdon 69), Ojai Valley (Thacher 34), Old Colony Mill (Brandegee in 1905), Visalia (Congdon in 1881), Placer Co. (Carpenter in 1892), Mendocino Co. (Vasey in 1875), Solano Co. (Jepson & Woolsey 4c; Jepson 4d; 4e), San Jacinto Mts. (Hall in 1901), Fresno Co. (Grant 1141), Yosemite Park (Hall 9675, with exceptionally large flowers), Nevada Falls (Redfield 5859), Placerville (Remy in 1855), Mare Island Bay (Wright in 1875), Napa Valley (Greene 335), Black Rock Mts. (Leiberg 5268), Butte Co. (Heller 11588), Madera Co. (Murdoc 2537), Mariposa Co. (Congdon in 1903). *Oregon;* Lakeview (Coville & Leiberg 150).

MEXICO: *Lower California* (Fish in 1882), Todos Santos (Fish in 1883).

Cuscuta salina Engelmann

C. salina Engelmann in Brewer, Watson & Gray, Bot. of Calif. Geol. Survey Publ., 1:536, 1880.

Stems very slender. Flowers glabrous, about 2.5–4.5 mm. long, pentamerous, on pedicels mostly shorter than the flowers in cymose

clusters; calyx lobes ovate to somewhat lanceolate, acute to acuminate, as long as the corolla tube; corolla campanulate, shallow or somewhat cylindrical; lobes as long as the tube, ovate to lanceolate acute to acuminate, upright, sometimes spreading; edges of the lobes frequently somewhat uneven, more or less overlapping; scales narrow, oblong, shorter than the tube, fringed with short processes, closely attached to the tube for nearly their entire length, sometimes with only the attachment to the filament fringed, bridged somewhat below the middle, or the scales reduced to small wings; anthers oval, on equal or shorter subulate filaments; styles slightly subulate, shorter than or equalling the globose, pointed ovary. Capsule globose, pointed, usually one-seeded, surrounded by the withered corolla; seeds about 1.5 mm. long, globose-ovoid, rostrate; hilum short, oval, transverse. Commonly found parasitizing saline herbs.

Cuscuta salina squamigera (Engelmann) n. comb.

[Figure 126]

C. californica squamigera Engelmann, Trans. Acad. Sci. St. Louis, 1:499, 1859.
C. subinclusa abbreviata Engelmann, Trans. Acad. Sci. St. Louis, 1:500, 1859.
C. squamigera (Engelmann) Piper, Contrib. U. S. Nat. Herb., 11:455, 1906.

Flowers relatively small, more narrowly campanulate than in the following variety; corolla slightly fleshy, the cells somewhat lens shape; lobes of the calyx and corolla ovate-lanceolate, acute.

Type locality: Rio Virgen, Utah. Range: British Columbia to California and Arizona. A doubtful specimen comes from Mexico.

Specimens examined: CANADA: *British Columbia;* Vancouver Island (Macoun 85812, 85818).

UNITED STATES: *Washington;* Temescal (Jepson 1570); San Juan Islands (Zeller 1129). *Utah;* Washington (Jones in 1880), St. George (Jones in 1880), Rio Virgen (Remy in 1855, the type of *C. californica squamigera*, a fragment in the Engelmann Herb.), southern Utah (Parry 206). *California* (Lemmon in 1878), San Jacinto Valley (Vasey 436), Solano Co. (Jepson 5a), Santa Barbara (Rothrock 101), San Bernardino Co. (Parish 2174, 6012), San Diego (Abrams 4015, Collins & Kempton 328), Long Beach (McClatchie in 1896), Vallejo (Greene 327), Santa Cruz (Jones in 1901, 2316), Oxnard (Burtt-Davy 7831½). *Arizona;* Tucson (Thornber 7516), Maricopa (Thornber in 1901), Sacaton (Thornber 2462).

MEXICO: *Tepic;* San Blas (?Maltby 21, fragmentary).

Cuscuta salina major n. var.

[Figures 32 a–e, 121 and 140]

Flowers larger than in the last, broadly campanulate; corolla lobes broadly ovate, acute, overlapping, spreading. The two varieties are closely united by intermediate forms.

Type locality: Palo Alto, California. Range: British Columbia to California, usually parasitizing *Salicornia*.

Specimens examined: CANADA: *British Columbia;* Crescent (Henry 4912, 4913), Vancouver Island, Victoria (Pineo, Macoun in 1887).

UNITED STATES: *Oregon;* Along coast (House 4683). *Washington* (Stevens in 1853), Port Angeles (Foster 1863), Union City (Piper 715), Westport (Cowles 520), Seattle (Zeller

in 1910). *California* (Kellog & Harford 779), San Francisco Bay (Hall 5721), Palo Alto (Baker 41, the type, in the N. Y. Bot. Gard. Herb.), Mendocino Co. (McMurphy 54), Santa Clara Co. (Elmer 1757), San Francisco (Bolander 2491), Bucksport (Tracy 3551), Mariposa (Congdon in 1901), Eureka (Hitchcock in 1915), Santa Cruz Mts. (Hitchcock 188), Humboldt Bay (Tracy 1256), San Diego (Brandegee, Berg in 1904), Head of San Joaquin Valley (Burtt-Davy 1966), San Mateo Co. (Abrams in 1906), Coronado (Berg in 1904), West Berkeley (Michener & Bioletti in 1891, Burtt-Davy in 1896, King in 1894), Los Angeles Co. (Chandler 2043), San Diego Co. (Parish 2281), Oakland (Congdon in 1904).

Cuscuta salina acuminata n. var.

[Figures 32 f–g and 89]

Perianth divisions lanceolate, acuminate. Scales apparently nearly absent or reduced to a very few lateral projections.

Type location: On an island of a mountain lake, Skamania Co., Washington.

Specimens examined: UNITED STATES: *Washington;* Skamania Co., on an island of a mountain lake (Suksdorf 1487, the type, in the U. S. Nat. Herb. as sheet 49,803). *California;* southeastern part (Purpus 5678).

Subsection LEPIDANCHE Engelmann

Cuscuta § Lepidanche Engelmann, Trans. Acad. Sci. St. Louis, 1:509, 1859.

Flowers pedicelled or sessile in compact clusters; calyx lobes free, surrounded by subtending bracts.

Key to the species

Flowers pedicelled, loosely paniculate, bracts numerous or few in the inflorescence, usually at least one subtending each flower ..... *C. cuspidata* (p. 72).

Flowers sessile in more or less dense clusters.

Bracts acute, closely appressed ..... *C. squamata* (p. 73).

Bracts acute, squarrose ..... *C. glomerata* (p. 74).

Bracts obtuse, closely appressed ..... *C. compacta* (p. 75).

Cuscuta cuspidata Engelmann

[Figures 49, 105 and 134]

C. cuspidata Engelmann, Bost. Journ. Nat. Hist., 5:224, 1847; and in Trans. Acad. Sci. St. Louis, 1:502, 1859.—Matthew, Bull. Torr. Bot. Club, 20, pl. 165. fig. 8, 1893.—Britton & Brown, Illustr. Flora, 3:30, fig. 2965, 1898; 2 ed., 3:51, fig. 3451, 1913.

C. cuspidata pratensis Engelmann, Bost. Journ. Nat. Hist., 5:224, 1847.

C. cuspidata humida Engelmann, Bost. Journ. Nat. Hist., 5:224, 1847.

Stems medium. Flowers glabrous, about 4 mm. long, pentamerous, membranous, pedicelled or subsessile in loose or dense panicled clusters, the whole inflorescence more or less bracteate; calyx of distinct or very slightly united segments, subtended by one or two ovate, orbicular, obtuse, sometimes cuspidate bracts, sepals of similar shape, obtuse or cuspidate, somewhat glandular thickened along the median portion and with the edges more or less serrulate; corolla funnel shape; lobes oblong, shorter than the tube, obtuse or with a mucronate or cuspidate tip, usually with a row of glandular cells along the median portion; scales oblong, shorter than the tube or reaching the filaments, fringed with medium length processes,

bridged at about the middle; styles slender and much longer than the globose-oblong or slightly conic ovary; stamens shorter than the lobes; anthers oval, somewhat cordate, slightly versatile, usually shorter than the filaments. Capsule globose, with a slightly thickened ridge or collar about the intrastylar aperture, frequently with numerous glandular cells, carrying the withered corolla at the apex; seeds about 1.4 mm. long, olive brown, slightly obovate, compressed or angular; hilum short, oblong or oval, oblique or nearly transverse.

When Engelmann described this species he segregated two varieties (variety *pratensis* and variety *humida*), a distinction that he did not maintain, however, in his later publications. It has been impossible to differentiate varieties although the forms included here show considerable variation in the number of bracts, texture of the flowers, etc.

Type locality: "Dry prairies west of the Brazos." Range: Mostly in the prairie states; from Illinois westward to Utah and Colorado and southward to Texas and Louisiana.

Specimens examined: UNITED STATES: Lat. 41° (Hall & Harbour 404). *Connecticut;* New Haven (Eaton, ex. Herb. Thurber in Herb. G. V. Nash. Seems typical, but probably not collected in Conn.). *Illinois;* St. Clair Co. (Eggert in 1878, in 1891), Mascoutah (Welsch), Cahokia (Eggert in 1874). *N. Dakota;* Towner (Lunell 842), McHenry Co. (Lunell in 1908). *S. Dakota;* Brookings Co. (Johnson in 1903). *Nebraska;* Valentine (Bates in 1895), Grant Co. (Rydberg 1639), Lincoln (Hannah in 1916), Nichols Co. (Hedgcock in 1889), Sand Hills of the Platte (Hayden in 1853–54). *Iowa;* Muscatine (Reppert in 1895). *Kansas;* Finney Co. (Hitchcock 359), Manhattan (Carleton in 1892), Tankton (without indication of collector, in 1892), Meade (Smyth 80a, c, e, f, g, i, k), Rockport (Bartholomew in 1889), Miami Co. (Oyster 5953), Bourbon Co. (Hall in 1867). *Missouri;* St. Louis (Eggert in 1891), Willard (Standley 9700, Blankinship in 1889 and in 1892), Malden (Bush in 1893), Kansas City (Bush 414), Campbell (Bush in 1893), Pacific (Thompson in 1898), Iron Co. (Russell in 1897). *Oklahoma* (DeBarr 460), Pottawatomie Co. (White in 1900). *Indian Territory* (Butler in 1875), Sapulpa (Bush 388, 1359). *Louisiana;* Lake Charles (Mackenzie 543). *New Mexico;* Arkansas River (Fendler 659b). *Texas* (Lindheimer 277), Victoria (Thurber 2), Dallas (Reverchon 664, 2194), Fort Smith to the Rio Grande (Bigelow 3, and in 1853–54), Polytechnic (Ruth 317), Randall Co. (Ball 1261), Moore Co. (Carleton 421), Austin Co. (Wurzlaw), Fort Worth (Reverchon 3202), Columbia (Bush 932), Brazoria Co. (Palmer 6684), on the Blanco (Wright in 1847), west of the Brazos (Lindheimer 125, taken as the type, in the Engelmann Herb.), between San Antonio & Victoria (Schott), Wilburger Co. (Eggert). *Colorado* (Parry 273). *Utah;* Ogden Hot Springs (Ries in 1893), North Ogden (Hillman).

Cuscuta squamata Engelmann
[Figures 51, 117 and 135]

C. squamata Engelmann, Trans. Acad. Sci. St. Louis, 1:510, 1859.

Stems slender. Flowers glabrous, pentamerous, sessile, few to several in separate or glomerate clusters, subtended by 2–10 ovate, acute, serrulated, sometimes cuspidate, closely appressed bracts that are shorter than the calyx; calyx lobes distinct, ovate, acute, cuspidate, closely appressed, somewhat serrulate, equalling the corolla tube, in appearance

much like the bracts; corolla cylindrical; lobes ovate, lanceolate, acute, sometimes somewhat cuspidate, spreading or reflexed; scales about reaching the filaments, oblong, their processes of medium length and numerous, bridged at about the middle; stamens shorter than the lobes; filaments as long as or shorter than the oblong-oval anthers; ovary globose to slightly conic, somewhat two-pointed; styles longer than the ovary; stigmas capitate. Capsule globose, slightly conical to pointed by the thickened apex, somewhat glandular on the upper portion, carrying the withered corolla at its apex; seeds about 1.5 mm. long, slightly oblique, one or infrequently two in a capsule, globose or compressed, brown, roughened; hilum short, linear, oblique.

Type locality: "Fields and wastes on the Rio Grande," Texas. Range: Texas, New Mexico and northern Mexico.

Specimens examined: UNITED STATES: *New Mexico;* Dona Ana Co. (Wooton in 1899 and in 1902, Standley 426, 6370 and in 1906, Standley & Wooton 336, in 1906 and in 1907), Chaves Co. (Earle & Earle 289). *Texas;* El Paso (Wright 392, 518, taken as the type, in the Engelmann Herb., 1628, Bigelow in 1852, Thurber 818, Jones 4170, in 1884, Stearns 455), Presidio Valley (Havard in 1881 and in 1883).

MEXICO: *Chihuahua* (Pringle 785), Presidio del Norte (Parry in 1852).

Cuscuta glomerata Choisy
[Figures 50, 120 and 137]

C. glomerata Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:280, pl. 4, fig. 1, 1841; and in DC., Prodromus, 9:458, 1845.—Engelmann, Trans. Acad. Sci. St. Louis, 1:510, 1859.—Matthew, Bull. Torr. Bot. Club, 20, pl. 165, fig. 12, 1893.—Britton & Brown. Illustr. Flora, 3:31, fig. 2967, 1898; 2 ed., 3:52, fig. 3453, 1913.

C. aphylla Rafinesque, Amer. Monthly Mag. & Crit. Rev., 4:40, 1818; not Loureiro 1790.

?C. paradoxa Rafinesque, Annals of Nature, 1:13, 1820.

C. americana Hooker, Comp. to the Bot. Mag., 1:173, 1835; not L. 1753.

?Anthanema paradoxa Rafinesque, Fl. Tellur., 4:90, 1836.

Lepidanche compositarum Engelmann, Amer. Journ. Sci. & Arts, 43?: 344, pl. 6, figs. 30–35, 1842.

L. compositarum solidaginis Engelmann, Amer. Journ. Sci. & Arts, 43:344, 1842.

L. compositarum helianthi Engelmann, Amer. Journ. Sci. & Arts, 43:344, 1842.

Stems medium, disappearing early from between the dense straw-colored, rope-like floral masses which are wound tightly about the stem of the host. Flowers glabrous, 4–5 mm. long, pentamerous, sessile, mostly endogenously formed, breaking forth in two parallel rows on opposite sides of the stem, much imbricated with numerous, scarious, lacerated, cupped, oblong, obtuse to acutish bracts with recurved tips; sepals distinct, oblong-oval, obtuse to acutish, their tips somewhat spreading but ordinarily not recurved, otherwise similar to the bracts; corolla cylindrical; lobes spreading or sometimes reflexed, oblong to lanceolate, obtuse or acutish, sometimes mucronate, usually with a row of glandular cells along the mid-portion, shorter than the corolla tube; scales shorter than the tube, oblong, more profusely fringed at the apex than along the

sides, bridged at about the middle or above; stamens shorter than the corolla lobes; anthers elliptical to oblong, about as long as or shorter than the filaments; styles capillary, longer than the somewhat flask-shaped ovary. Capsule globose-pointed or flask-shaped with the withered corolla carried at its apex; seeds about 1.7 mm. long, oval, globose, slightly compressed, light brown, one or infrequently two in the capsule, or this not infrequently sterile; hilum oblong, oval, transverse.

This is undoubtedly the plant referred to by Rafinesque and named *C. aphylla* by him. His name would be valid were it not that Loureiro in 1790 used *aphylla* to designate another plant of this group. It is rather doubtful if the plant described by Rafinesque as *C. paradoxa* is the same as this one.

Type location: "Hab. prope St. Louis in Missouri." Range: Throughout the prairie states from Indiana and Michigan westward to S. Dakota and Nebraska and southward to Mississippi and Texas.

Specimens examined: UNITED STATES: *Michigan;* Berrien Co. (Pepoon 936), Cass Co. (Pepoon 300). *Indiana;* Whiting (Chase 422), McCallon's (Clapp in 1837), New Albany (Clapp in 1836), Lake Maxinkuckee (Clark in 1909), Wells Co. (Deam in 1901). *Tennessee;* Henderson (Bain in 1892), Dickson Co. (Gattinger in 1886), Chester Co. (Bain 331). *Illinois;* Winnebago Co. (Bebb in 1859), Naperville (Umbach in 1896), Mt. Carmel (Schneck in 1877), Herod (Clinton 28756), Ringwood (Vasey), Thornton (without indication of collector, in 1865), Henderson Co., Oquawka (Patterson), Aurora (Boyce in 1883), Ravinia (Sherff in 1911), Springfield (Spencer in 1919), Fountaindale (Bebb in 1872), Alton (Douglass in 1891), Iroquois Co. (Moffatt 526), Riverside (Greenman in 1912), So. Chicago (Sherff 1755), Glencoe (Greenman 2881), St. Clair Co. (Eggert in 1875). *Wisconsin;* Walworth Co. (Shannon 127). *Minnesota;* Morton (McMillan in 1890), Zumbrota (Ballard in 1892). *S. Dakota;* Clay Co. (Over 5131), Yankton (Dean in 1861). *Nebraska* (Hayden in 1853), Weeping Water (Williams 40), Newark (Hopeman in 1893), Ashland (Williams in 1889), Nicholls Co (Hedgcock in 1899), Holt Co., Turkey Creek (Clements 2819), Lincoln (Hannah in 1916). *Iowa;* Decatur Co. (Fitzpatrick in 1897), Ames (Pammel & Ball 79, Hitchcock in 1888), Spirit Lake (Cratty in 1901). *Missouri;* Willard (Blankinship in 1887), Kirksville (Sheldon in 1884), Webb City (Palmer 818, 3069), Lawrence (Blankinship in 1895), Desoto (Hasse in 1887), St. Louis (Engelmann 417, in 1841, in 1864, Eggert in 1880, Craig in 1911, Riehl 15, taken as the type, a specimen with the type number in the Engelmann Herb., 16, also cited by Choisy with the type), Springfield (Weller 66, Standley in 1905, 8456, 9156), Prosperity (Palmer 3861), Jasper Co. (Bush in 1893), Green Co. (Blankinship in 1889), Jackson Co. (Bush in 1893), Joplin (Palmer 3129). *Kansas;* Riley Co. (Norton 360), Manhattan (without indication of collector or date, Kellerman in 1890), Lawrence (Stevens), Wichita (Smyth 250b, 250c), Pawnee Fork of Ark. river (Fendler 657), Pottawatomie Co., St. George (Kellerman in 1890). *Mississippi;* Oktibbeha Co. (Pollard 1280), Harman Lake (Tracy 1649). *Indian Territory* (Sheldon 263, Baker in 1875, Butler 13), Sapulpa (Bush 389), Limestone Gap (Butler 111, 11235). *Texas* (Lindheimer 10), Commanche Spring (Lindheimer 1028), Llano (Lindheimer in 1847), Fort Smith to Rio Grande (Bigelow 5), Dallas Co. (Reverchon 1686), Gillespie Co. (Williams 753).

Cuscuta compacta Jussieu

C. compacta Jussieu in Choisy, Mém. Soc. Phys. et Hist. Nat. Genève, 9:281, pl. 4, fig. 2, 1841; and in DC., Prodromus, 9:458, 1845.—Engelmann, Trans. Acad. Sci. St Louis,

1:511, 1859.—Matthew, Bull. Torr. Bot. Club, 20, pl. 165, fig. 11, 1893.—Britton & Brown, Illustr. Flora, 3:31, fig. 2966, 1898; 2 ed., 3:52, fig. 3452, 1913.

Stems coarse. Flowers glabrous, 4–5 mm. long, pentamerous (infrequently tri- or tetramerous), sessile, in compact clusters about the host or somewhat more loose; sepals distinct, orbicular to oval, cupped, sometimes fringed with short, slender, filamentous processes, surrounded by 3–5 similar, appressed bracts; cells of the bracts and sepals with heavily thickened walls; corolla tube cylindrical, becoming urceolate in fruit; lobes spreading to reflexed, oblong, obtuse, infrequently fringed with short, filamentous processes, much shorter than the tube; scales shorter than the tube or reaching the filaments, fringed with long processes, bridged at about the middle, small scales frequently appearing on the bridge between the larger ones, or the scales much reduced; stamens shorter than the lobes; anthers oval, about equal to or longer than the short, thick filaments; ovary globose, conical, thickened at the apex. Capsule globose-conic, slightly pointed, glandular about the apex which carries the withered corolla; seeds about 2.6 mm. long, globose, ovate, angled or flattened on one side, scurfy; hilum oblong, oblique.

Cuscuta compacta typica

[Figures 54 a–e, 106 and 131]

?C. acaulis Rafinesque, Annals of Nature, 1:13, 1820.

C. remotiflora Bertoloni, Misc. Bot., 10:29, 1842.—Engelmann, Trans. Acad. Sci. St. Louis, 1:511, 1859; in synon.

C. fruticum Bertoloni, Misc. Bot., 10:29, 1842.—Engelmann, Trans. Acad. Sci. St. Louis, 1:511, 1859; in synon.

Lepidanche adpressa Engelmann, Amer. Journ. Sci. & Arts, 45:77, 1843.

C. compacta adpressa Engelmann, Trans. Acad. Sci. St. Louis, 1:511, 1859.

C. coronata Beyrich in Engelmann, Trans. Acad. Sci. St. Louis, 1:511, 1859; in synon.

C. imbricata Nuttall in Engelmann, Trans. Acad. Sci. St. Louis, 1:511, 1859; in synon.

C. americana of various authors, Engelmann, Trans. Acad. Sci. St. Louis, 1:511, 1859; in synon.

Corolla nearly enclosed in the calyx or somewhat exserted; scales well developed. The common form.

Type locality: "Hab. Amer. septentrionalem." Range: From New Hampshire, Connecticut and Massachusetts southward to Florida and westward through the central and southern states to Arkansas, Oklahoma and Texas.

Specimens examined: UNITED STATES: *New Hampshire;* Derry (Seaman). *Massachusetts;* Marion (Vail in 1888). *Connecticut;* New Haven (Eaton in 1858). *New Jersey;* Ocean Co. (Mackenzie 2908, Redfield 5851 and in 1874), West New York (Van Sickle in 1894), Landisville (Gross 2193), Atsion (Allen in 1879), Merchantsville (Redfield 5845), Pine Barrens (Canby 2). *District of Columbia;* Takoma Park (Chase 2571), Washington (Holm in 1888, Steele in 1896 and in 1902, Blanchard in 1891). *Maryland;* Salisbury (Tidestrom 7446), Hyattsville (Steele in 1904). *Virginia;* Franklin (Heller 1166), Carlins (Dewey 37), southeast Va. (Kearney 2365), Alexandria (Shull 204, 367). *N. Carolina;* Jackson Co. (Ashe), Elizabeth City (Boettcher 293), Buncombe Co. (Gray & Sullivant in 1863), Swain

Co. (Beardslee & Kofoid in 1891); Biltmore (Biltmore Herb. 3735g). *S. Carolina;* Aiken (Ravenel in 1874). *Tennessee;* Cocke Co. (Kearney 844, 845), Tullohoma (Gattinger in 1886), Jackson (Bain 438), Green Co. (Redfield 5652), Hiawassee (Ruth in 1895), McFarland (Ruth in 1893), Hollow Rock (Eggert in 1897). *Kentucky;* Edmunson Co. (Price in 1897). *Alabama;* Mobile (Mohr in 1896), Auburn (Lloyd & Earle in 1900); Cullman (Eggert in 1897 and in 1898). *Florida* (Chapman) Apalachicola (without indication of collector, Herb. Chapman 3735b), Duval Co. (Curtiss 2193), Jacksonville (Curtiss 5328), St. Vincent Island (McAtee 1807a), Tallahassee (Berg), Lake City (Rolfs 508, 510). *Georgia* (Beyrich, the type of *C. coronata*, a fragment in the Engelmann Herb.), Stone Mt. (Hitchcock in 1905), Walton Co. (Small in 1894), Habersham Co. (Small in 1893). *Louisiana;* Alden Bridge (Trelease in 1898), Shreveport (Gregg in 1847). *Mississippi;* between Gulf Port & Long Beach (Joor in 1891). *Indiana;* Sullivan Co. (Deam 29369), Lawrence Co. (Deam 18499), Jackson Co. (Deam 9520), Posey Co. (Deam 24280, 29076), Dubois Co. (Deam 28253). *Illinois;* E. Carondelet (Eggert in 1891), Mt. Carmel (Schneck in 1887), Opposite St. Louis (Engelmann in 1845), Peoria (Brendel). *Missouri;* St. Louis (Eggert in 1891, Engelmann in 1842, the type of *Lepidanche adpressa*, in the Engelmann Herb. taken as the type), Allenton (Letterman in 1879), Howell Co. (Bush in 1892), Carter Co. (Trelease 477), Monteer Co. (Bush 218, 371, 5143), Scott Co. (Eggert in 1894). *Arkansas;* Hot Springs (Palmer 8476, Letterman, Trelease in 1898), Hempstead Co. (Palmer 6840), Magnet Cove (Trelease in 1897), Howard Co. (Kellogg in 1909). *Oklahoma;* (Page 2641), Leflore Co. (Stevens 2641). *Indian Territory;* Cherokee Nation (Blankinship in 1895). *Texas* (Wright, Thuron in 1890), Dallas (Reverchon 3201), Sheldon (Reverchon 3883).

Cuscuta compacta efimbriata n. var.

[Figure 54 f]

Tube much exserted; scales shorter than the tube and much reduced, bifid or winged and with few processes.

Type locality: Duval Co., Florida. Range: Known only from the type locality.

Specimens examined: UNITED STATES: *Florida;* Duval Co. (Fredholm 305, the type, in the U. S. Nat. Herb. as sheet 214,815).

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EXPLANATION OF PLATES

PLATES I–IX

Each species is represented by drawings of a flower, an opened corolla, an opened calyx, a capsule (an ovary was sketched in a few species in which mature capsules were not available), and a separately drawn scale for those species possessing scales. In some of the species made up of different varieties drawings of the floral parts showing varietal differences have been included. The drawings are enlarged about five diameters with the exception of the individual scales which are enlarged about ten diameters. The scales represented on the opened corollas were drawn from outlines and no attempt was made to make them accurate in all details. The drawings of the individual scales, however, was made to show the details correctly.

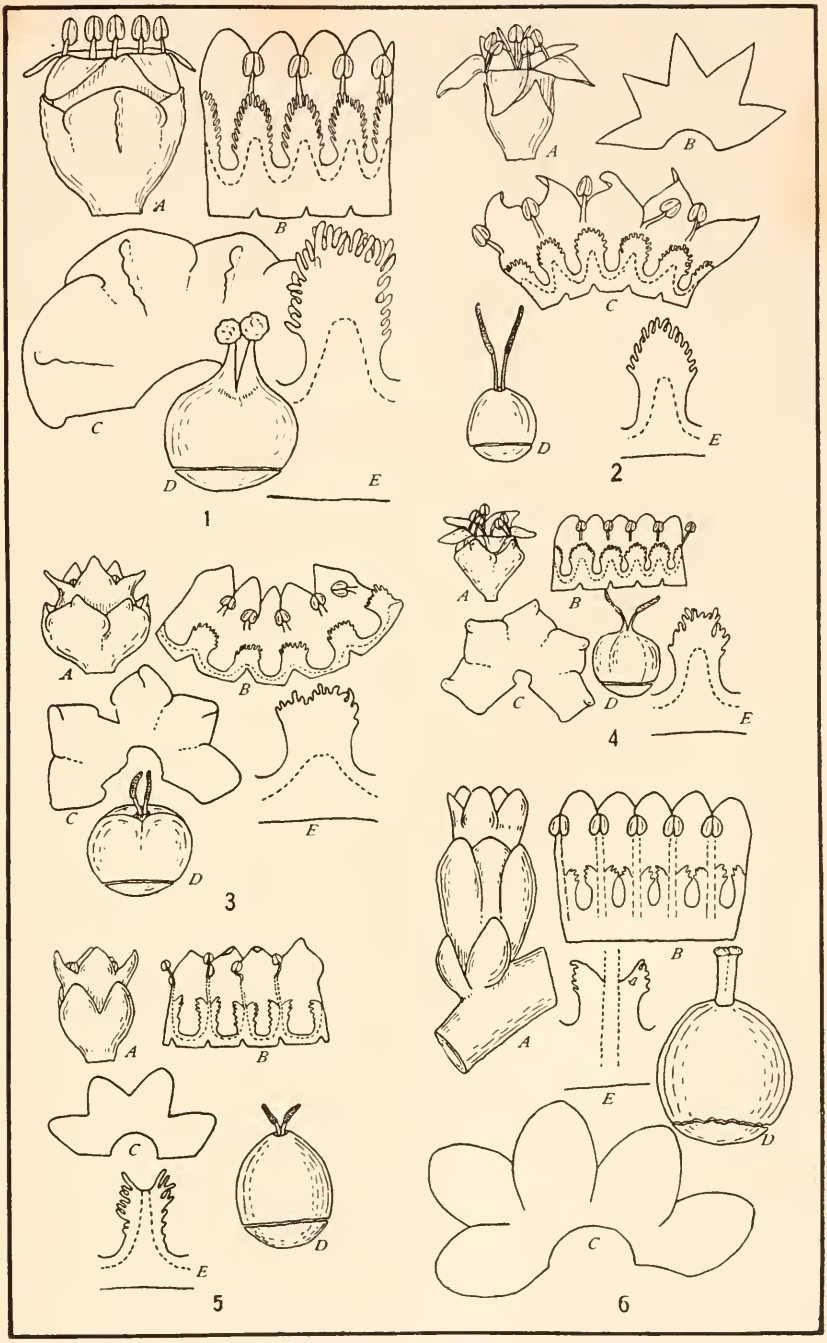
PLATES X–XIII

Besides the drawings, photographs of the flowers, capsules and seeds of many of the species are included. These are enlarged about five diameters.

PLATE I

EXPLANATION OF PLATE

Fig. 1, a-e—*Cuscuta rugosiceps*
Fig. 2, a-e—*Cuscuta epithymum*
Fig. 3, a-e—*Cuscuta epilinum*
Fig. 4, a-e—*Cuscuta planiflora*
Fig. 5, a-e—*Cuscuta europaea*
Fig. 6, a-e—*Cuscuta exaltata*

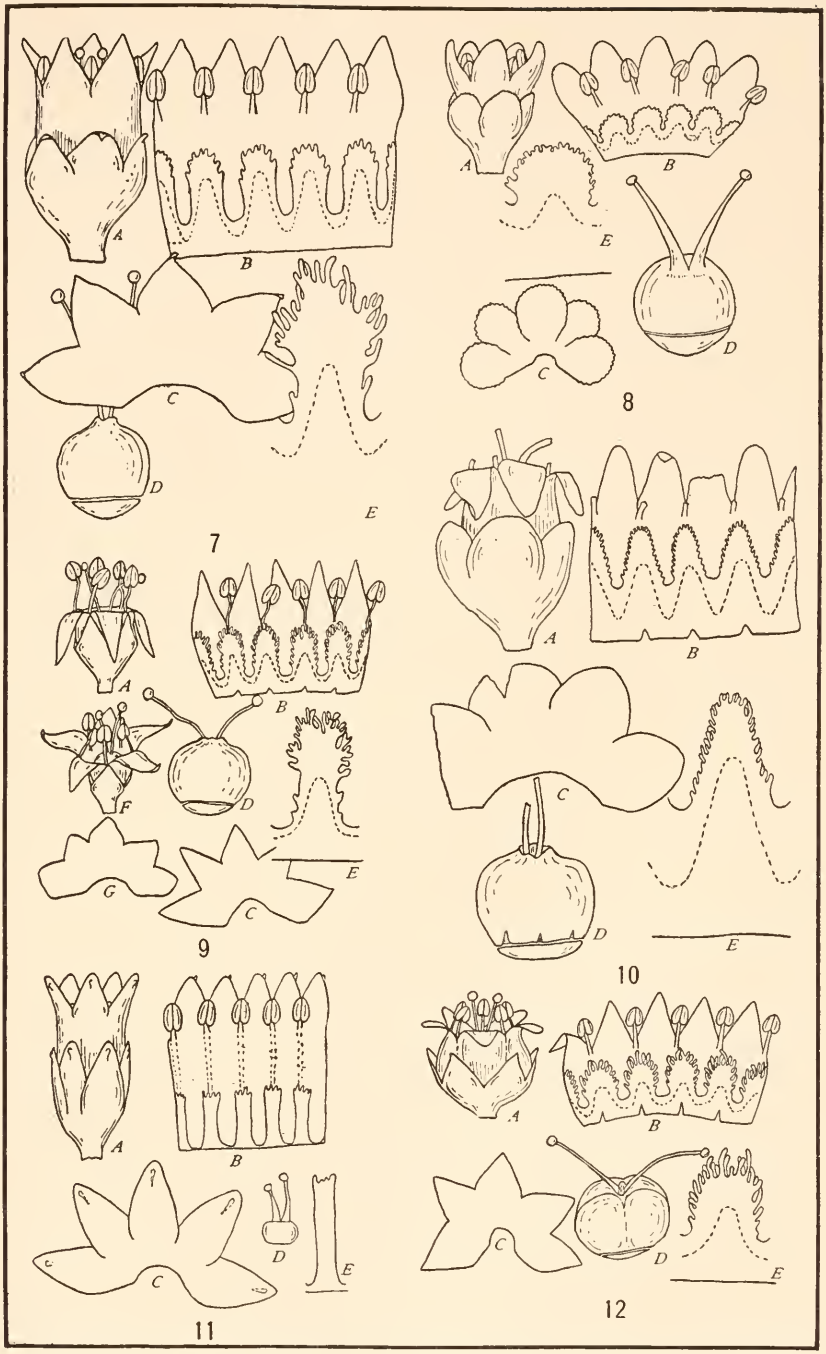


YUNCKER AMERICAN-WEST INDIAN CUSCUTA PLATE I

PLATE II

EXPLANATION OF PLATE

Fig. 7, a–d—*Cuscuta odontolepis typica*
Fig. 7, e —*Cuscuta odontolepis fimbriata*
Fig. 8, a–e—*Cuscuta erosa*
Fig. 9, a–e—*Cuscuta umbellata typica*
Fig. 9, f–g—*Cuscuta umbellata dubia*
Fig. 10, a–e—*Cuscuta floribunda*
Fig. 11, a–e—*Cuscuta chapalana* (d represents the ovary)
Fig. 12, a–e—*Cuscuta partita*

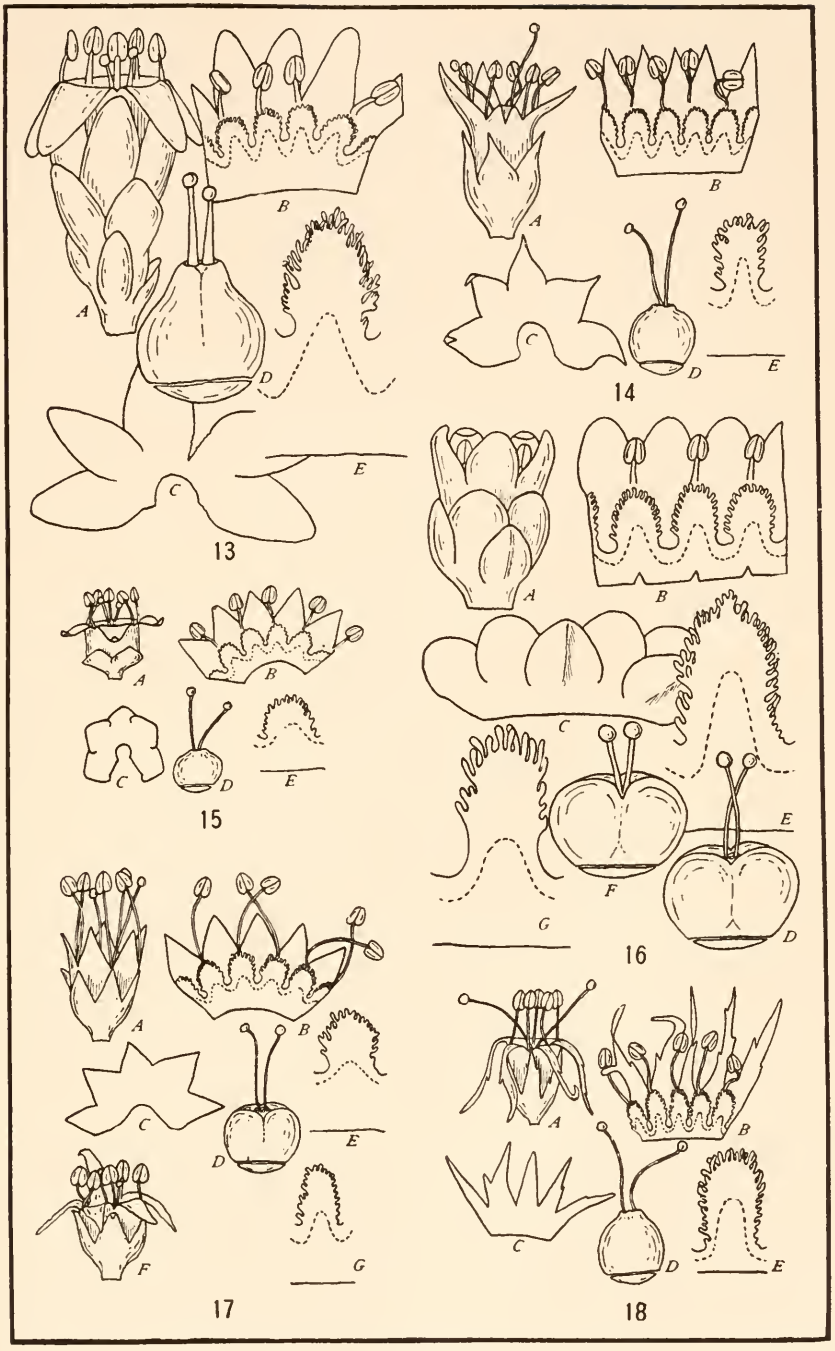


YUNCKER AMERICAN-WEST INDIAN CUSCUTA PLATE II

PLATE III

EXPLANATION OF PLATE

Fig. 13, a–e—*Cuscuta pringlei*
Fig. 14, a–e—*Cuscuta choisiana*
Fig. 15, a–e—*Cuscuta deltoidea*
Fig. 16, a–e—*Cuscuta tinctoria typica*
Fig. 16, f–g—*Cuscuta tinctoria kellermaniana*
Fig. 17, a–e—*Cuscuta gracillima subtilis*
Fig. 17, f–g—*Cuscuta gracillima saccharata*
Fig. 18, a–e—*Cuscuta lacerata*

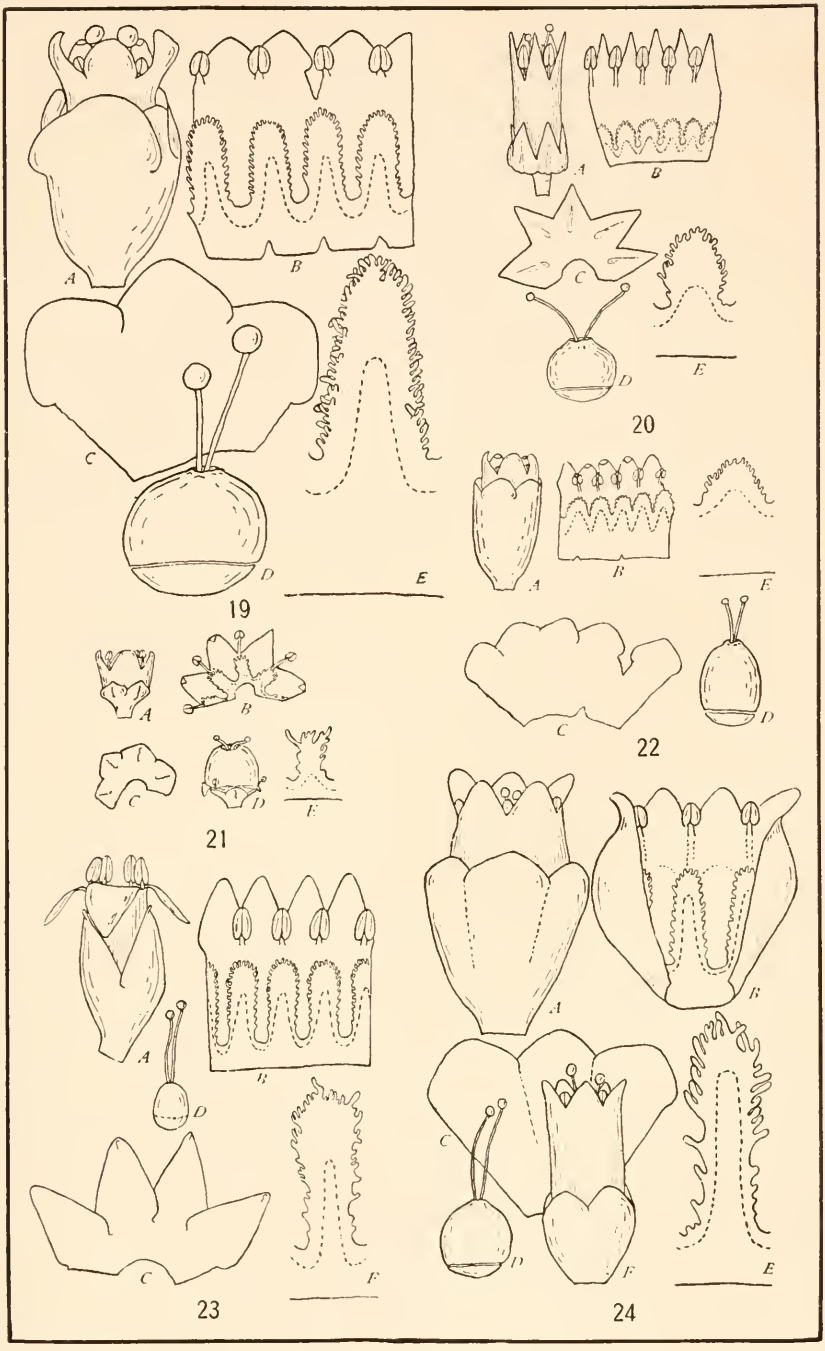


YUNCKER AMERICAN-WEST INDIAN CUSCUTA PLATE III

PLATE IV

EXPLANATION OF PLATE

Fig. 19, a–e—*Cuscuta macrocephala*
Fig. 20, a–e—*Cuscuta tuberculata*
Fig. 21, a–e—*Cuscuta harperi*
Fig. 22, a–e—*Cuscuta americana*
Fig. 23, a–e—*Cuscuta purpusii* (d represents the ovary)
Fig. 24, a–e—*Cuscuta corymbosa grandiflora*
Fig. 24, f —*Cuscuta corymbosa stylosa*

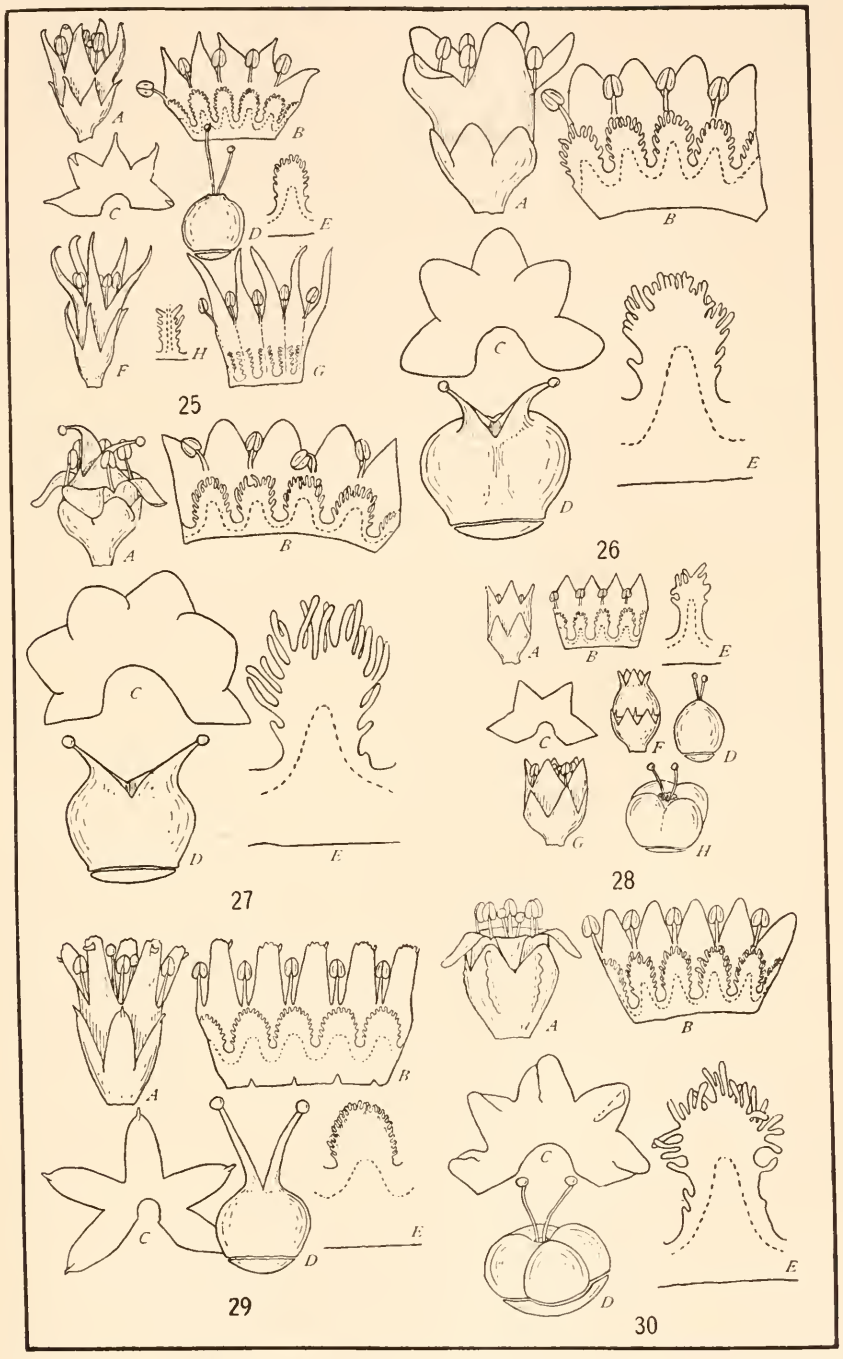


YUNCKER AMERICAN–WEST INDIAN CUSCUTA PLATE IV

PLATE V

EXPLANATION OF PLATE

Fig. 25, a–e—*Cuscuta desmouliniana typica*
Fig. 25, f–h—*Cuscuta desmouliniana attenuiloba*
Fig. 26, a–e—*Cuscuta jalapensis*
Fig. 27, a–e—*Cuscuta mitraeformis*
Fig. 28, a–f—*Cuscuta potosina typica*
Fig. 28, g–h—*Cuscuta potosina globifera*
Fig. 29, a–e—*Cuscuta ceratophora*
Fig. 30, a–e—*Cuscuta applanata*

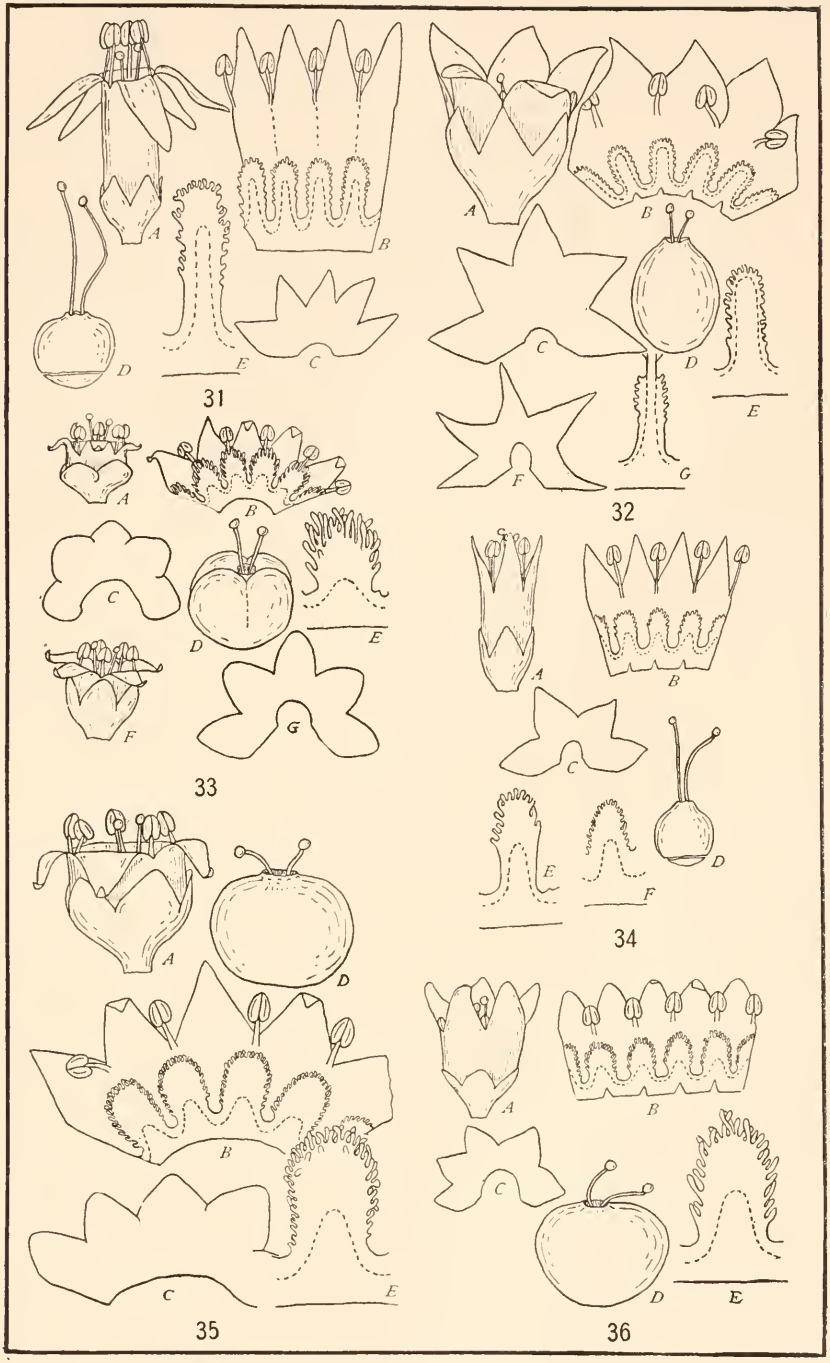


YUNCKER AMERICAN-WEST INDIAN CUSCUTA PLATE V

PLATE VI

EXPLANATION OF PLATE

Fig. 31, a–e—*Cuscuta polyanthemos*
Fig. 32, a–e—*Cuscuta salina major*
Fig. 32, f–g—*Cuscuta salina acuminata*
Fig. 33, a–e—*Cuscuta pentagona typica*
Fig. 33, f–g—*Cuscuta pentagona calycina*
Fig. 34, a–e—*Cuscuta leptantha typica*
Fig. 34, f —*Cuscuta leptantha palmeri*
Fig. 35, a–e—*Cuscuta plattensis*
Fig. 36, a–e—*Cuscuta racemosa chiliana*

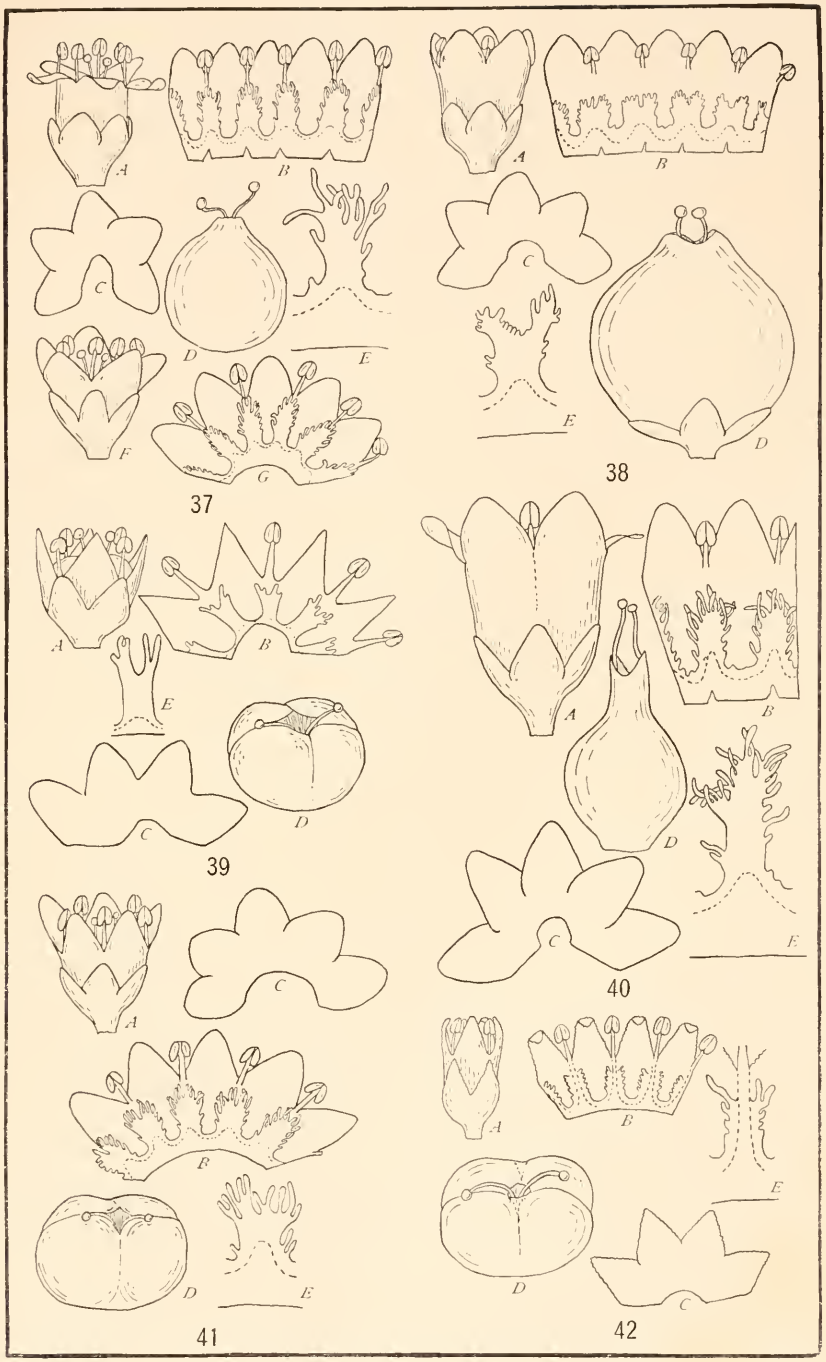


YUNCKER AMERICAN–WEST INDIAN CUSCUTA PLATE VI

PLATE VII

EXPLANATION OF PLATE

Fig. 37, a–e—*Cuscuta gronovii vulgivaga*
Fig. 37, f–g—*Cuscuta gronovii latiflora*
Fig. 38, a–e—*Cuscuta curta*
Fig. 39, a–e—*Cuscuta polygonorum*
Fig. 40, a–e—*Cuscuta rostrata*
Fig. 41, a–e—*Cuscuta glandulosa*
Fig. 42, a–e—*Cuscuta coryli*

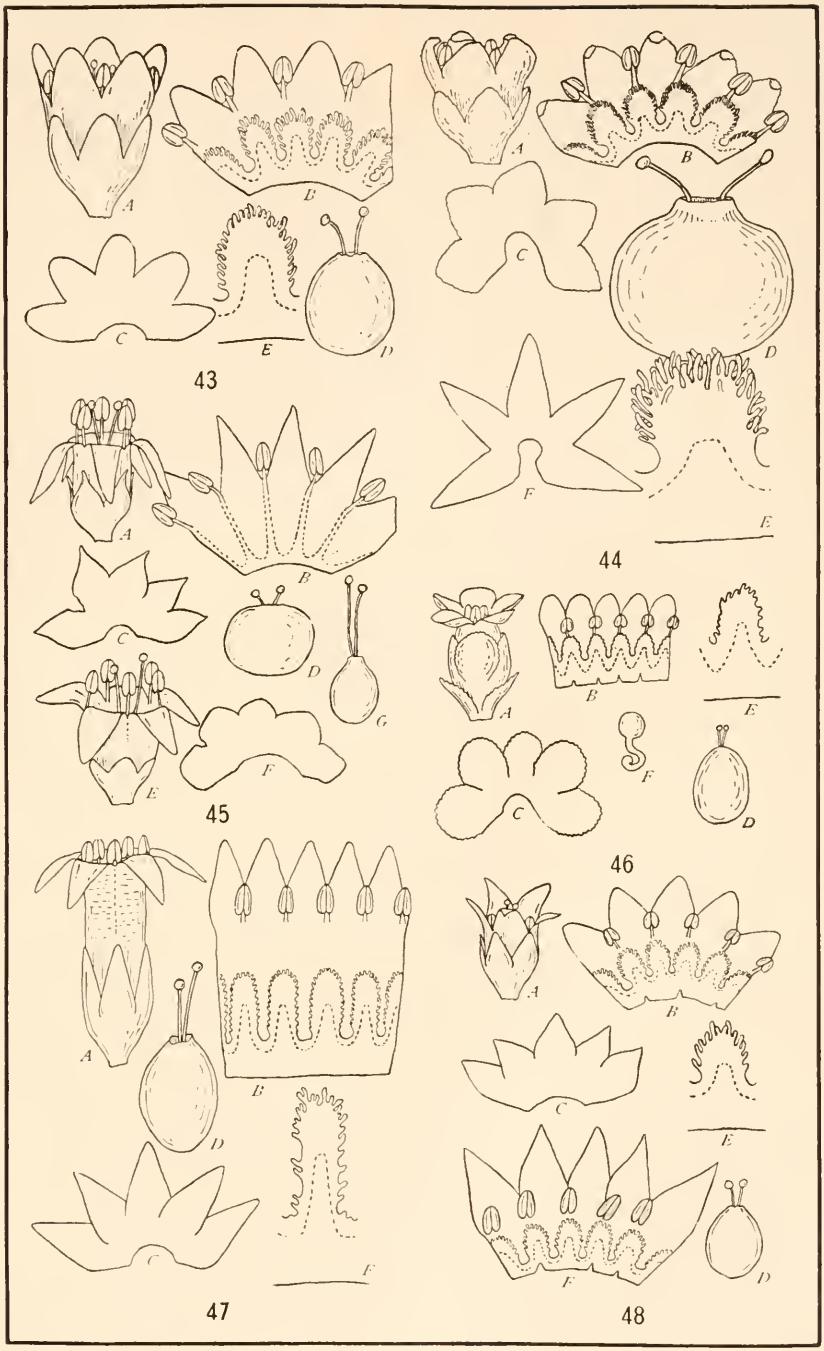


YUNCKER AMERICAN–WEST INDIAN CUSCUTA PLATE VII

PLATE VIII

EXPLANATION OF PLATE

Fig. 43, a–e —*Cuscuta decipiens*
Fig. 44, a–e —*Cuscuta indecora neuropetala*
Fig. 44, f —*Cuscuta indecora longisepala*
Fig. 45, a–c —*Cuscuta californica graciliflora*
Fig. 45, d —*Cuscuta californica breviflora*
Fig. 45, e–f —*Cuscuta californica brachycalyx*
Fig. 45, g —*Cuscuta californica apiculata*
Fig. 46, a–f —*Cuscuta denticulata* (f represents the embryo)
Fig. 47, a–e—*Cuscuta subinclusa*
Fig. 48, a–e—*Cuscuta veatchii typica*
Fig. 48, f —*Cuscuta veatchii apoda*

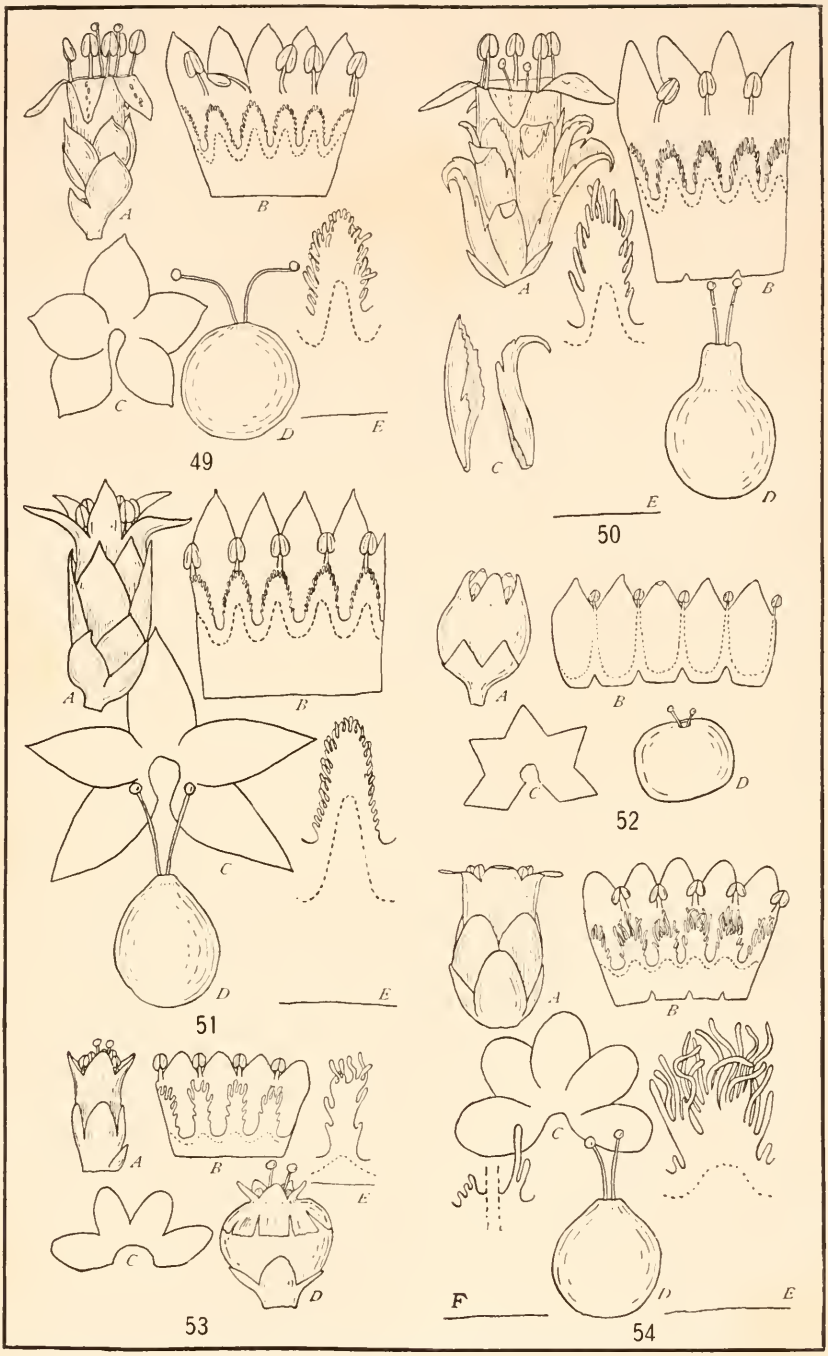


YUNCKER AMERICAN–WEST INDIAN CUSCUTA PLATE VIII

PLATE IX

EXPLANATION OF PLATE

Fig. 49, a–e—*Cuscuta cuspidata.*
Fig. 50, a–e—*Cuscuta glomerata*
Fig. 51, a–e—*Cuscuta squamata*
Fig. 52, a–d—*Cuscuta jepsonii*
Fig. 53, a–e—*Cuscuta cephalanthi*
Fig. 54, a–e—*Cuscuta compacta typica*
Fig. 54, f —*Cuscuta compacta efimbriata*

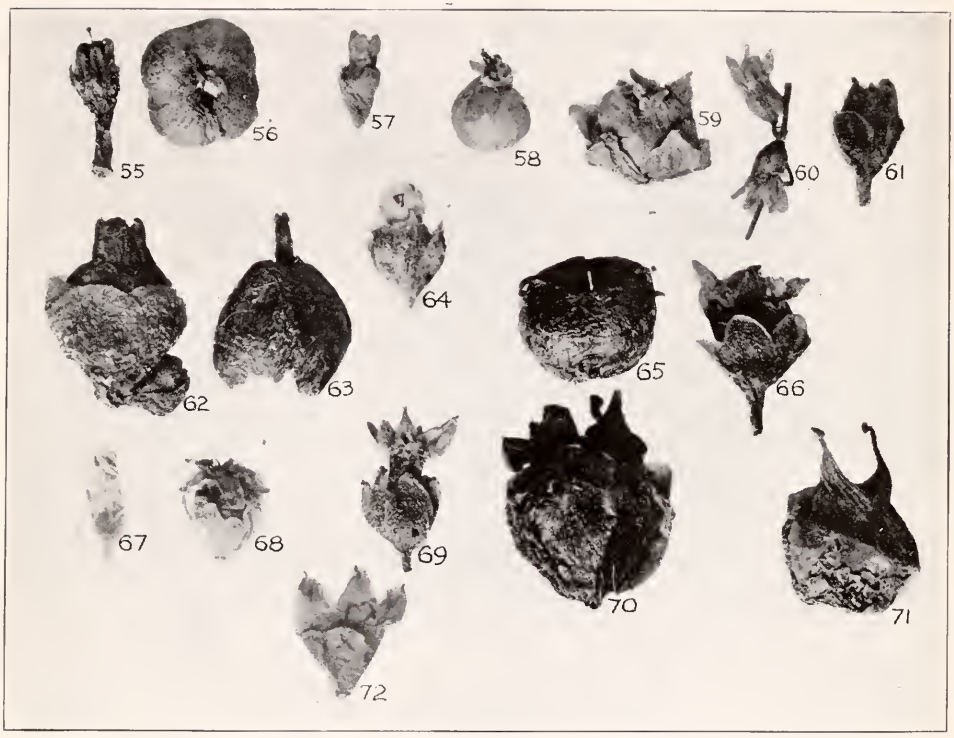


YUNCKER AMERICAN-WEST INDIAN CUSCUTA PLATE IX

PLATE X

EXPLANATION OF PLATE

Fig. 55—*Cuscuta coryli* flower
Fig. 56—*Cuscuta coryli* capsule
Fig. 57—*Cuscuta cephalanthi* flower
Fig. 58—*Cuscuta cephalanthi* capsule
Fig. 59—*Cuscuta epilinum* flower
Fig. 60—*Cuscuta veatchii typica* flowers
Fig. 61—*Cuscuta erosa* flower
Fig. 62—*Cuscuta exaltata* flower
Fig. 63—*Cuscuta exaltata* capsule
Fig. 64—*Cuscuta planiflora* flower
Fig. 65—*Cuscuta jalapensis* capsule
Fig. 66—*Cuscuta jalapensis* flower
Fig. 67—*Cuscuta desmouliniana typica* flower
Fig. 68—*Cuscuta applanata* flower
Fig. 69—*Cuscuta chapalana* flower
Fig. 70—*Cuscuta rugosiceps* flower
Fig. 71—*Cuscuta mitraeformis* capsule
Fig. 72—*Cuscuta ceratophora* flower

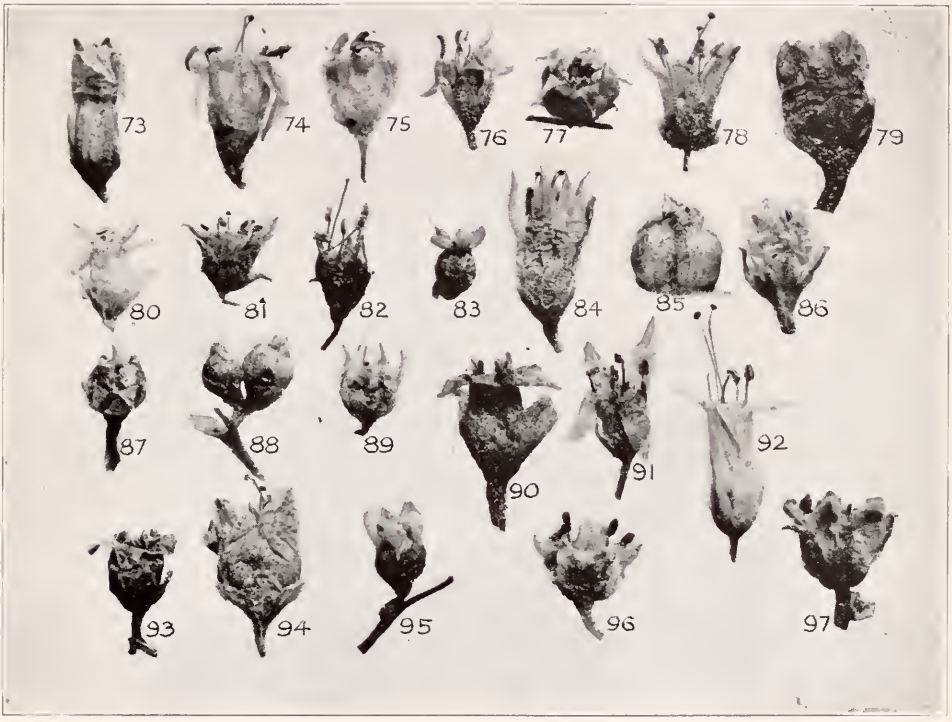


YUNCKER AMERICAN–WEST INDIAN CUSCUTA PLATE X

PLATE XI

EXPLANATION OF PLATE

Fig. 73—*Cuscuta subinclusa* flower
Fig. 74—*Cuscuta californica graciliflora* flower
Fig. 75—*Cuscuta californica brachycalyx* flower
Fig. 76—*Cuscuta californica papillosa* flower
Fig. 77—*Cuscuta californica breviflora* flower
Fig. 78—*Cuscuta tuberculata* flower
Fig. 79—*Cuscuta tinctoria typica* flower
Fig. 80—*Cuscuta chaisiana* flower
Fig. 81—*Cuscuta gracillima saccharata* flower
Fig. 82—*Cuscuta gracillima subtilis* flower
Fig. 83—*Cuscuta denticulata* flower
Fig. 84—*Cuscuta californica graciliflora* flower
Fig. 85—*Cuscuta europaea* capsule with corolla at top
Fig. 86—*Cuscuta epithymum* flower
Fig. 87—*Cuscuta potosina globifera* flower
Fig. 88—*Cuscuta potosina typica* capsules with corollas at top
Fig. 89—*Cuscuta salina acuminata* flower
Fig. 90—*Cuscuta purpusii* flower
Fig. 91—*Cuscuta leptantha palmeri* flower
Fig. 92—*Cuscuta polyanthemos* flower
Fig. 93—*Cuscuta decipiens* flower
Fig. 94—*Cuscuta racemosa chiliana* flower
Fig. 95—*Cuscuta decipiens* flower
Fig. 96—*Cuscuta indecora neuropetala* flower
Fig. 97—*Cuscuta indecora longisephala* flower

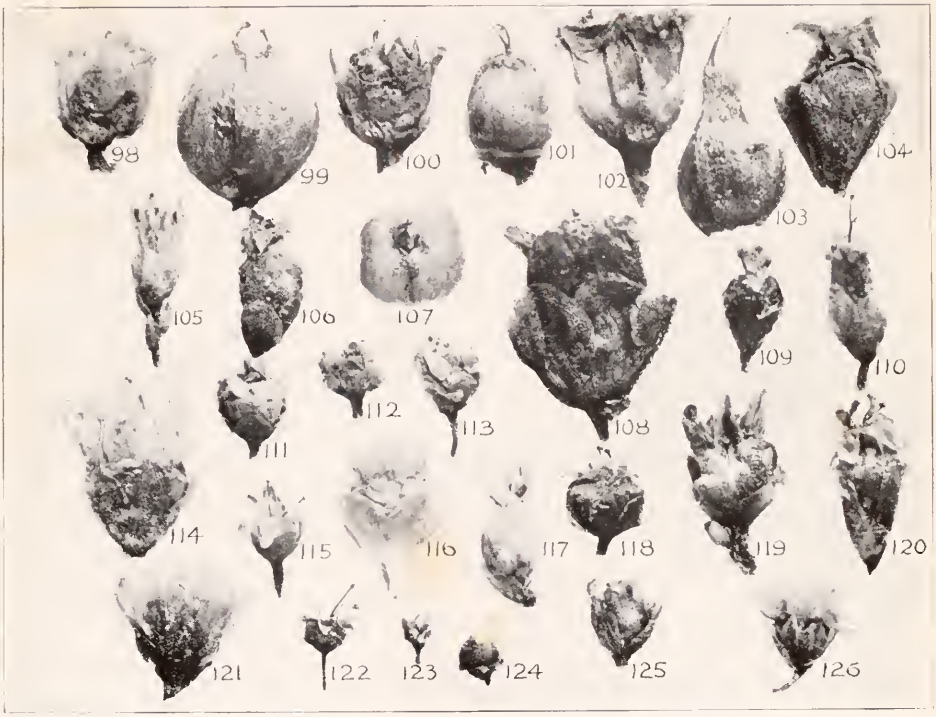


YUNCKER AMERICAN-WEST INDIAN CUSCUTA PLATE XI

PLATE XII

EXPLANATION OF PLATE

Fig. 98—*Cuscuta curta* flower
Fig. 99—*Cuscuta curta* capsule
Fig. 100—*Cuscuta gronovii vulgivaga* flower
Fig. 101—*Cuscuta gronovii vulgivaga* capsule
Fig. 102—*Cuscuta rostrata* flower
Fig. 103—*Cuscuta rostrata* capsule
Fig. 104—*Cuscuta corymbosa grandiflora* flower
Fig. 105—*Cuscuta cuspidata* flower
Fig. 106—*Cuscuta compacta typica* flower
Fig. 107—*Cuscuta polygonorum* capsule
Fig. 108—*Cuscuta macrocephala* flower
Fig. 109—*Cuscuta americana congesta* flower
Fig. 110—*Cuscuta corymbosa stylosa* flower
Fig. 111—*Cuscuta pentagona verrucosa* flower
Fig. 112—*Cuscuta pentagona typica* flower
Fig. 113—*Cuscuta pentagona calycina* flower
Fig. 114—*Cuscuta umbellata reflexa* flower
Fig. 115—*Cuscuta umbellata typica* flower
Fig. 116—*Cuscuta odontolepis typica* flower
Fig. 117—*Cuscuta squamata* flower
Fig. 118—*Cuscuta partita* flower
Fig. 119—*Cuscuta pringlei* flower
Fig. 120—*Cuscuta glomerata* flower
Fig. 121—*Cuscuta salina major* flower
Fig. 122—*Cuscuta deltoidea* flower
Fig. 123—*Cuscuta harperi* flower
Fig. 124—*Cuscuta harperi* capsule
Fig. 125—*Cuscuta glandulosa* flower
Fig. 126—*Cuscuta salina squamigera* flower



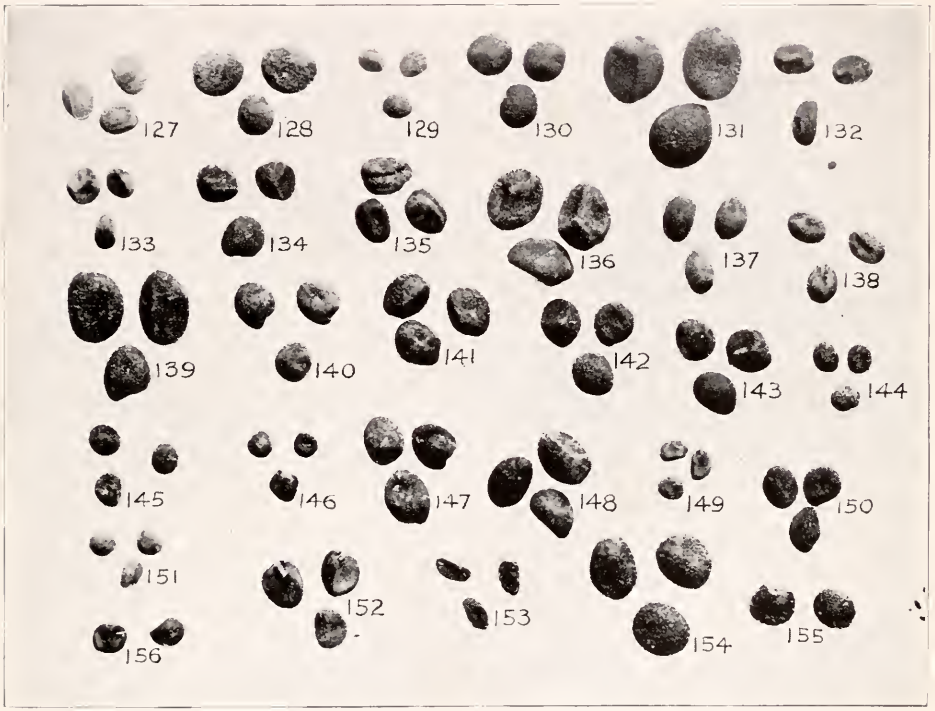
YUNCKER AMERICAN-WEST INDIAN CUSCUTA PLATE XII

PLATE XIII

EXPLANATION OF PLATE

Seeds

Fig. 127—*Cuscuta pentagona*
Fig. 128—*Cuscuta indecora*
Fig. 129—*Cuscuta planiflora*
Fig. 130—*Cuscuta coryli*
Fig. 131—*Cuscuta compacta*
Fig. 132—*Cuscuta applanata*
Fig. 133—*Cuscuta epilinum*
Fig. 134—*Cuscuta cuspidata*
Fig. 135—*Cuscuta squamata*
Fig. 136—*Cuscuta curta*
Fig. 137—*Cuscuta glomerata*
Fig. 138—*Cuscuta americana*
Fig. 139—*Cuscuta rostrata*
Fig. 140—*Cuscuta salina*
Fig. 141—*Cuscuta mitraeformis*
Fig. 142—*Cuscuta cephalanthi*
Fig. 143—*Cuscuta glandulosa*
Fig. 144—*Cuscuta europaea*
Fig. 145—*Cuscuta epithymum*
Fig. 146—*Cuscuta denticulata*
Fig. 147—*Cuscuta subinclusa*
Fig. 148—*Cuscuta gronovii*
Fig. 149—*Cuscuta umbellata*
Fig. 150—*Cuscuta polygonorum*
Fig. 151—*Cuscuta californica*
Fig. 152—*Cuscuta pringlei*
Fig. 153—*Cuscuta odontolepis*
Fig. 154—*Cuscuta mitraeformis*
Fig. 155—*Cuscuta rugosiceps*
Fig. 156—*Cuscuta partita*



YUNCKER AMERICAN-WEST INDIAN CUSCUTA PLATE XIII

INDEX OF COLLECTIONS

ABRAMS
1560; 2654. C. californica graciliflora
2230. C. pentagona calycina
4015. C. salina squamigera
(1906). C. salina major
ABRAMS & MCGREGOR
505; 522. C. denticulata
ALLEN
(1879). C. compacta typica
ANDERSON
1385. C. gronovii vulgivaga
(1894). C. californica graciliflora
ANDREWS
(1890). C. coryli
(1890; 1898). C. cephalanthi
(1892; 1898). C. polygonorum
ANDRIEUX
214. C. corymbosa stylosa
ANTHONY
266. C. californica graciliflora
ARMSTRONG
(1892). C. gronovii vulgivaga
ASHCRAFT
(1895). C. gronovii vulgivaga
ASHE
..... C. pentagona typica
..... C. rostrata
..... C. compacta typica
AUSTIN
492. C. subinclusa
BAIN
331; (1892). C. glomerata
338; (1894). C. gronovii vulgivaga
438. C. compacta typica
BAKER
41. C. salina major
57; 3954. C. subinclusa
555. C. indecora neuropetala
1477. C. planiflora
1560. C. californica graciliflora
1761. C. pentagona calycina
(1875). C. glomerata
(1918). C. exaltata
BALL
919. C. indecora neuropetala
1261. C. cuspidata
(1890). C. rostrata
BALLARD
(1892). C. glomerata
BANKER
556. C. gronovii vulgivaga
BARBER
(1898). C. gronovii vulgivaga
BARLOW
(1900). C. gronovii vulgivaga
BARTHOLOMEW
(1889). C. cuspidata
BARTLET
691; 696. C. pentagona typica
BARTWELL
..... C. gronovii vulgivaga
BATES
698. C. pentagona typica
(1895). C. cuspidata
(1896). C. coryli
(1896). C. indecora neuropetala
BEAL
(1869). C. pentagona typica
BEARDSLEE
(1876). C. cephalanthi
(1876). C. gronovii vulgivaga
BEARDSLEE & KOFOID
(1891). C. rostrata
(1891). C. compacta typica
BEBB
(1859; 1872). C. glomerata
BECHDOLT
(1889). C. epithymum
BECK
..... C. epilinum
BELL
(1867). C. curta
BENTHAM
..... C. americana congesta
..... C. americana spectabilis
..... C. corymbosa grandiflora
BERG
(1904). C. salina major
..... C. compacta typica
BERLANDIER
822. C. corymbosa stylosa
865; 965; 2285. C. indecora hispidula
1103. C. corymbosa grandiflora
2457; (1827). C. pentagona verrucosa

BERNOULLI
59. C. corymbosa grandiflora
BEYRICH
175–2; ..... C. coryli
(1845). C. pentagona typica
..... C. compacta typica
BIGELOW
1; 9. C. pentagona typica
3; (1853–54). C. cuspidata
5. C. glomerata
8. C. coryli
(1850). C. glandulosa
(1851). C. exaltata
(1851). C. umbellata typica
(1852). C. squamata
(1854). C. californica apiculata
BILTMORE HERBARIUM
2126a. C. gronovii vulgivaga
3735g. C. compacta typica
3736a. C. indecora neuropetala
5727; 5727a; 5727b. C. rostrata
BIOLETTI
(1892). C. subinclusa
BISCHOFF
(1848). C. gronovii vulgivaga
BISKY
(1886). C. pentagona typica
BISSELL
47; 78; 158; 1900. C. epithymum
(1904). C. pentagona typica
BLANCHARD
(1890). C. pentagona typica
(1891). C. compacta typica
BLANKINSHIP
407. C. pentagona calycina
(1887; 1889; 1895). C. glomerata
(1889; 1892). C. cuspidata
(1889). C. pentagona typica
(1895). C. compacta typica
(1895). C. gronovii latiflora
(1895). C. gronovii vulgivaga
(1900). C. coryli
BLODGETT
(1903). C. pentagona typica
BODIN
230. C. coryli
BOETTCHER
122. C. pentagona typica
293. C. compacta typica
BOLANDER
2436; 2674; 2698; 2849; 6381. C. subinclusa
2491. C. salina major
2673. in part. C. europaea
2673. in part. C. indecora neuropetala
5055. C. californica breviflora
BOLDINGH
5481; 7081. C. partita
BOND
(1891). C. pentagona typica
BONPLAND
..... C. floribunda
BOURGEAU
(1866). C. corymbosa stylosa
BOYCE
(1883). C. glomerata
BOYKIN
(1838). C. glandulosa
BRADY
(1896). C. gronovii vulgivaga
BRANDEGEE
4; ..... C. pentagona calycina
7; (1889; 1892; 1905); ..... C. californica graciliflora
404; (1893; 1915). C. tuberculata
406. C. leptantha palmeri
407. C. umbellata typica
409; (1890; 1897; 1904). C. macrocephala
704. C. curta
(1869). C. gronovii vulgivaga
(1889). C. veatchii typica
(1890; 1897; 1905). C. californica breviflora
(1892); ..... C. indecora neuropetala
(1892; 1894; 1905). C. subinclusa
(1893). C. americana congesta
(1893). C. gracillima esquamata
(1893; 1902; 1904). C. umbellata reflexa
(1897). C. planiflora
(1904). C. applanata
(1904). C. polyanthemos
(1909). C. denticulata
(1913; 1915). C. veatchii apoda
(1914); ..... C. californica brachycalyx
..... C. salina major
BRAUNTON
(1902). C. subinclusa
BRENDEL
(1880); ..... C. coryli
(1892). C. polygonorum
..... C. compacta typica
..... C. cephalanthi
BREWER
68; 1292 in part; 2698. C. subinclusa

1283; 1292 in part. C. californica graciliflora

BRIDGES
..... C. subinclusa

BRIGGS
1509. C. cephalanthi

BRINTON
(1888). C. gronovii vulgivaga

BRITTON
1910; 3006; 3897. C. americana congesta
3102. C. umbellata typica
3798. C. pentagona calycina

BRITTON, BRITTON & MARBLE
2227. C. americana spectabilis

BRITTON, BRITTON & SHAFER
43. C. americana congesta
137. C. americana spectabilis

BRITTON, BRITTON & WILSON
5507. C. indecora neuropetala

BRITTON & COWELL
306. C. pentagona calycina

BRITTON, COWELL & BRITTON
2109. C. glandulosa
5379. C. americana spectabilis

BRITTON, COWELL & BROWN
4676; 4794; 4978. C. umbellata typica

BRITTON, COWELL & SHAFER
12887. C. americana congesta

BRITTON, EARLE & WILSON
5917. C. americana congesta

BRITTON & FISHLOCK
1101. C. americana spectabilis

BRITTON & HOLLICK
1737. C. umbellata typica

BRITTON & MILLSPAUGH
2208; 2811; 5519; 5925; 5963. C. americana congesta

BRITTON & SHAFER
707. C. americana spectabilis
1866. C. umbellata typica
2915. C. partita
3065. C. americana congesta
3069. C. ceratophora

BRITTON & WHEELER
224. C. americana spectabilis

BRITTON, WILSON & LEON
15321. C. americana congesta

BRITTON, WILSON & SELBY
14493. C. americana congesta

BROADWAY
(1905). C. americana congesta

BROOMFIELD
(1847). C. umbellata typica

BROTHERTON
(1898). C. gronovii vulgivaga

BROWN
132. C. indecora neuropetala
492. C. planiflora

BUCKLEY
(1841; 1844). C. gronovii vulgivaga
(1842). C. rostrata

BUFFUM
1405. C. indecora neuropetala

BURNHAM
37. C. gronovii vulgivaga
(1895; 1901). C. coryli

BURTT-DAVY
1941. C. californica graciliflora
1966; (1896). C. salina major
7831½ C. salina squamigera

BUSH
6; 28; 202; 327; 411; 1815; 3244; (1892). C. coryli
63; 138; 1007; 1062; (1892; 1893). C. pentagona typica
215; 387; 812; 1011; 1067; 1416; 1509; 1568; 1569; 4909; 7868; (1888; 1893). C. gronovii vulgivaga
218; 371; 5143; (1892). C. compacta typica
262; (1892). C. cephalanthi.
388; 414; 932; 1359; (1893). C. cuspidata
389; (1893). C. glomerata
1405. C. glandulosa
1535. C. indecora hispidula
1750; 3013; 4068; 5855. C. pentagona calycina

BUSH & PALMER
3063. C. pentagona calycina

BUSTAMENTE
83. C. jalapensis

BUTLER
2; (1877). C. indecora longisepala
4. C. pentagona verrucosa
13; 111; 11235. C. glomerata
15. C. californica breviflora
19; 50; 94; 11236. C. coryli
536. C. planiflora
(1875). C. cuspidata

CAMP
(1893). C. cephalanthi

CAMPBELL
(1897). C. gronovii vulgivaga

CANBY
2. C. compacta typica
3. C. gronovii vulgivaga
(1862). C. cephalanthi
(1863; 1895). C. pentagona typica
(1876; 1880; 1884; 1888). C. rostrata
(1886). C. coryli
..... C. epilinum
CANNON
172. C. rostrata
CAREY
..... C. gronovii vulgivaga
CARLETON
421; (1892). C. cuspidata
CARPENTER
(1892). C. subinclusa
CHALMOT
..... C. gronovii vulgivaga
CHANDLER
423. C. californica breviflora
485. C. polygonorum
2010; 5199; 5384; (1897). C. californica graciliflora
2043. C. salina major
7123; 7124. C. subinclusa
CHAPMAN
..... C. pentagona typica
..... C. compacta typica
CHAPMAN HERBARIUM
3735b. C. compacta typica
(1863). C. glandulosa
CHASE
169; 600; 1181; 2626; (1896). C. gronovii vulgivaga
422. C. glomerata
522; (1894; 1896); ..... C. coryli
1982. C. cephalanthi
2532. C. polygonorum
2571. C. compacta typica
CHENEY
(1889). C. polygonorum
CHESTNUT
(1887). C. subinclusa
CHESNUT & DREW
(1888). C. indecora neuropetala
CHICKERING
(1873). C. pentagona typica
(1877; 1880). C. rostrata
CLAPP
(1836; 1837). C. glomerata
CLARK
4264. C. gronovii vulgivaga
(1909). C. glomerata
CLEMENTS
2799. C. coryli
2799½ C. gronovii vulgivaga
2819. C. glomerata
CLINTON
11794; 11795; 11796; 28574; 30449; 30450. C. cephalanthi
28756. C. glomerata
30438. C. polygonorum
(1864). C. coryli
(1864); ..... C. gronovii vulgivaga
..... C. epilinum
COCKERELL
20. C. applanata
COCKS
..... C. gronovii vulgivaga
COLLINS & KEMPTON
315. C. californica graciliflora
328. C. salina squamigera
COLORADO STATE AGRICULTURAL COLLEGE HERBARIUM
1541. C. indecora neuropetala
COMBS
546. C. americana congesta
COMMONS
5850; (1863). C. epilinum
CONGDON
65; 66. C. californica brachycalyx
69; (1881; 1903). C. subinclusa
(1901; 1904). C. salina major
(1902). C. pentagona calycina
COOK
(1887). C. gronovii vulgivaga
COOLEY
(1882). C. gronovii vulgivaga
COOPER
421. C. indecora neuropetala
(1901). C. cephalanthi
COPELAND
73. C. subinclusa
COUES & PALMER
246. C. indecora hispidula
COULTER
1010. C. umbellata typica
(1874). C. pentagona typica
(1876). C. polygonorum
COVILLE
(1895). C. gronovii vulgivaga
COVILLE & FUNSTON
102, 338. C. californica graciliflora
COVILLE & LEIBERG
150. C. subinclusa
175. C. californica breviflora

COWLES
520. C. salina major
CRAIG
(1908). C. coryli
(1911). C. glomerata
CRATTY
(1901). C. glomerata
CURRAN
(1883; 1888). C. denticulata
CURTISS
2188; 5840; 5881; (1843). C. pentagona typica
2193; 5328. C. compacta typica
(1845); ..... C. gronovii vulgivaga
(1845). C. rostrata
CUSICK
2341. C. planiflora
2347. C. californica breviflora
DANIELS
426. C. indecora neuropetala
696. C. pentagona calycina
DASH
628. C. americana congesta
DAVIS
561. C. epithymum
(1876; 1879). C. cephalanthi
(1889; 1892). C. gronovii vulgivaga
(1908). C. racemosa chiliana
DAY
64. C. gronovii vulgivaga
409. C. epithymum
DEAM
190; 444; 512; 9817; 14856. C. coryli
490; 1582; 5363; 5364 in part; 9889; 15304; 15382; 15476; 26482; (1899; 1903; 1905). C. cephalanthi
5364 in part; 5473; 7600; 9535; 12129; 12225; 14701; 14888; 15339; 18784; 21696; 22339; 23800; 23860; 24014; 26391; 26575; 26831; 28267; 29812; 30240; (1897; 1903; 1904; 1906). C. gronovii vulgivaga
7101; 9871; 12403; 17384; 25430; 28370; 28400. C. pentagona typica
9520; 18499; 24280; 28253; 29076; 29369. C. compacta typica
15269; 22182; (1903). C. polygonorum
(1901). C. glomerata
DEAN
(1861). C. glomerata
DEBARR
460. C. cuspidata
DEWART
(1892). C. coryli
(1892). C. cephalanthi
DEWEY
37. C. compacta typica
(1902). C. epilinum
DICK
(1890; 1895). C. gronovii vulgivaga
DODGE
104; 372; (1896). C. coryli
DOUGLASS
(1891). C. glomerata
DRUMMOND
III 247. C. pentagona verrucosa
..... C. pentagona calycina
DRUSHELL
(1916). C. coryli
DUBOIS
(1888). C. cephalanthi
DUDLEY
(1882). C. coryli
(1882). C. cephalanthi
DUFFEY
(1889). C. gronovii vulgivaga
DUGÈS
(1880). C. odontolepis fimbriata
DUSS, PÈRE
1878; 2468. C. americana congesta
EAMES
(1894). C. gronovii vulgivaga
EARLE & EARLE
289. C. squamata
EASTWOOD
91. C. pentagona calycina
129; (1890). C. indecora neuropetala
EATON
(1858). C. compacta typica
..... C. cuspidata
EBERT
(1893). C. umbellata reflexa
EGGERT
(1874; 1878; 1891); ..... C. cuspidata
(1875; 1880). C. glomerata
(1877). C. indecora neuropetala
(1877). C. gronovii latiflora
(1878; 1886; 1891; 1893). C. gronovii vulgivaga
(1878). C. polygonorum
(1879; 1886; 1897). C. coryli
(1879; 1891; 1896; 1897). C. pentagona typica

(1891; 1894; 1897; 1898). C. compacta typica

EGGLESON
7649. C. subinclusa
12247. C. pentagona typica
12249. C. gronovii vulgivaga

ELLIS
221; 224. C. curta

ELMER
1757. C. salina major
4543. C. californica breviflora

ELY
(1888). C. pentagona typica

ENGELMANN
417; (1841; 1864). C. glomerata
(1841; 1842; 1843; 1860). C. coryli
(1841; 1843; 1845). C. gronovii latiflora
(1841; 1842; 1860; 1879). C. cephalanthi
(1842; 1845). C. compacta typica
(1845). C. indecora neuropetala
(1856; 1876). C. gronovii vulgivaga
(1876). C. pentagona typica
(1880). C. erosa
(1880). C. odontolepis typica
(1880). C. subinclusa
(1880). C. umbellata reflexa

FARWELL
1291. C. coryli

FAVRAT
41. C. americana congesta

FAY
(1914). C. planiflora

FENDLER
657. C. glomerata
658. C. coryli
659b. C. cuspidata

FERNALD
88. C. gronovii vulgivaga

FERNALD & WEATHERBY
259. C. pentagona typica

FERNON
1896. C. umbellata typica

FINK
207; 632. C. cephalanthi
305. C. gronovii vulgivaga

FISH
(1882; 1883). C. subinclusa

FISHER
147. C. indecora neuropetala

FISHLOCK
489. C. americana spectabilis

FITZPATRICK
25. C. coryli
(1897). C. glomerata

FOSTER
1863. C. salina major
(1901). C. gronovii vulgivaga

FOWLER
(1880; 1884; 1892; 1894). C. gronovii vulgivaga

FREDHOLM
305. C. compacta efimbriata
3304. C. indecora hispidula

FREMONT
79. C. curta

FRETZ
(1882). C. gronovii vulgivaga

FUERTES
117; 916; 975b. C. indecora neuropetala
194. C. americana spectabilis

FURBISH
(1897). C. europaea

GALEOTTI
1412. C. corymbosa stylosa

GARBER
1883. C. umbellata typica
(1911). C. coryli

GARDNER
(1901). C. californica breviflora

GARRETT
192; 1714; 1716; 1719; 2692; 2736. C. indecora neuropetala
1002. C. planiflora
2170. C. californica breviflora
2213. C. cephalanthi

GATTINGER
(1879). C. pentagona typica
(1881). C. polygonorum
(1886). C. compacta typica
(1886). C. glomerata
(1886). C. gronovii vulgivaga
(1886). C. cephalanthi

GAUMER
705. C. americana spectabilis

GAYLE
811. C. gronovii vulgivaga

GEYER
674. C. pentagona calycina
(1841). C. gronovii latiflora
(1842). C. coryli
(1842). C. gronovii vulgivaga
(1842). C. pentagona typica
..... C. cephalanthi

GOLL
565; 711. C. americana spectabilis
GOODDING
509. C. pentagona calycina
724. C. indecora neuropetala
2296. C. veatchii apoda
2482. C. umbellata typica
GRABENDORFER
(1899). C. tuberculata
GRAHAM
250. C. jalapensis
GRANT
1141. C. subinclusa
3629; (1901). C. pentagona calycina
5217. C. cephalanthi
GRAY & SULLIVANT
(1843). C. coryli
(1843). C. gronovii vulgivaga
(1853). C. rostrata
(1863). C. compacta typica
GREEN
275. C. leptantha typica
12953; (1880). C. umbellata typica
(1880). C. tuberculata
GREENE
327. C. salina squamigera
335. C. subinclusa
978. C. indecora neuropetala
1046. C. racemosa chiliana
(1913). C. curta
GREENMAN
1477; 1478; 1825; 2138; 2695. C. gronovii vulgivaga
2782; 3800. C. coryli
2881; (1912). C. glomerata
GREGG
401; 417. C. pentagona verrucosa
490; ..... C. umbellata typica
570. C. tinctoria
(1847). compacta typica
(1849). C. americana congesta
..... C. gronovii calyptrata
GRIFFITHS
2044. C. umbellata reflexa
2155. C. indecora neuropetala
GRIFFITHS & SLOSSER
38; 105. C. gronovii vulgivaga
235. C. pentagona calycina
302; (1894). C. coryli
GRIFFITHS & THORNBER
21. C. odontolepis typica
GROSS
2193. C. compacta typica
(1882). C. pentagona typica
HAHN
18. C. corymbosa grandiflora
HALE
(1860–61). C. coryli
HALL
2; (1860). C. gronovii vulgivaga
3. C. curta
4. C. coryli
491; 493 in part. C. indecora hispidula
492; 493 in part. C. pentagona verrucosa
493 in part. C. indecora longisepala
5721. C. salina major
9094. C. californica breviflora
9219; (1897); ..... C. californica gracilis-flora
9675; (1901). C. subinclusa
(1861; 1867). C. cephalanthi
(1867). C. cuspidata
(1901). C. californica papillosa
HALL & HARBOUR
404. C. cuspidata
464. C. indecora neuropetala
HAMILTON
16. C. americana spectabilis
HANNAH
(1916). C. cuspidata
(1916). C. glomerata
(1916). C. polygonorum
HANSEN
1275. C. subinclusa
HARBOUR
464. C. pentagona calycina
HARGER
(1891). C. pentagona typica
HARPER
147. C. harperi
209; 224; 1650. C. indecora neuropetala
HARRIS
6975. C. americana congesta
HARRISON
(1888). C. gronovii vulgivaga
HARSHBERGER
(1904). C. gronovii vulgivaga
HARTMAN
52. C. odontolepis typica
179. C. tuberculata
236. C. americana congesta

HARVEY & HARVEY
699; (1895). C. gronovii vulgivaga
HARWOOD
(1901). C. gronovii vulgivaga
HASSE
(1882). C. gronovii vulgivaga
(1887). C. glomerata
(1890). C. subinclusa
(1892). C. californica papillosa
HAVARD
2. C. pentagona calycina
4. C. leptantha typica
(1881; 1883). C. squamata
HAYDEN
26. C. coryli
(1853). C. glomerata
(1853). C. cuspidata
(1853). C. pentagona typica
..... C. cephalanthi
HAYS
..... C. umbellata typica
HEADLY
(1907). C. indecora neuroptela
HEDGCOCK
(1889). C. cuspidata
(1894). C. cephalanthi
(1899). C. glomerata
(1901). C. pentagona calycina
HEDRICK
(1899). C. pentagona calycina
HEIZER
345. C. planiflora
HELLER
1135. C. pentagona calycina
1166. C. compacta typica
1549. C. pentagona verrucosa
1899; 6169. C. americana spectabilis
9684. C. californica breviflora
11588. C. subinclusa
11677. C. indecora neuropetala
HELLER & HALBACH
1357. C. gronovii vulgivaga
HEMMICK
4. C. gronovii vulgivaga
HENDERSON
2892. C. indecora neuropetala
(1884). C. cephalanthi
HENRY
4912; 4913. C. salina major
HERMANN, v.
686. C. glandulosa
HERRICK
(1904). C. pentagona calycina
HEYDE
287. C. tinctoria
HEYDE & LUX
2912. C. tinctoria
HILL
66–1876. C. curta
68–1909. C. epithymum
76–1871; 128–1905. C. pentagona typica
81–1884; 134–1882; 151–1871. C. gronovii vulgivaga
95–1876; 100–1897; 120–1897; 124–1897. C. coryli
(1891). C. cephalanthi
(1891). C. polygonorum
HILLMAN
(1891). C. denticulata
(1899); ..... C. planiflora
(1904). C. pentagona typica
(1904; 1905). C. coryli
..... C. cuspidata
..... C. pentagona calycina
..... C. polygonorum
..... C. racemosa chiliana
HIORAM, BRO.
2279. C. americana spectabilis
HITCHCOCK
188; (1915). C. salina major
205; (1915). C. subinclusa
232; (1904). C. gronovii vulgivaga
359. C. cuspidata
(1888). C. glomerata
(1890). C. americana congesta
(1894). C. cephalanthi
(1905). C. compacta typica
(1905); ..... C. pentagona typica
(1905). C. rostrata
(1910). C. epithymum
(1915); ..... C. californica graciliflora
HOLLISTER
120. C. gronovii vulgivaga
HOLM
(1888). C. compacta typica
(1893). C. pentagona typica
HOLMES
17188. C. pentagona typica
HOLTON
..... C. americana spectabilis
HOLZINGER
(1888). C. polygonorum

(1888). C. gronovii vulgivaga
(1889). C. cephalanthi

HOPEMAN
(1893). C. glomerata

HORN
2849; (1863). C. subinclusa

HORNER
373. C. californica breviflora
639. C. pentagona calycina

HOUSE
4683. C. salina major

HOVEY
..... C. coryli
..... C. gronovii vulgivaga

HOWARD
(1888). C. leptantha typica

HOWELL
336. C. pentagona calycina
(1884). C. californica breviflora

HUMBOLDT
..... C. umbellata typica

HURST
(1890). C. planiflora

JACOBS
(1888). C. cephalanthi

JAMES
..... C. umbellata typica

JEPSON
3b; 3c; 4a; 4d; 4e; 70a; 70b; 125b; 1735; (1892). C. subinclusa
5a; 1570. C. salina squamigera
5b; 5d; (1891). C. californica brachycalyx
5c. C. jepsonii
70c; 1704. C. californica graciliflora
80a; 125a. C. californica apodanthera
1628. C. californica papillosa
(1893). C. racemosa chiliana

JEPSON & WOOLSEY
4c. C. subinclusa

JERMY
34. C. pentagona pubescens
74; 75. C. indecora neuropetala
(1904). C. exaltata

JOHNSON
399. C. indecora neuropetala
(1888). C. coryli
(1900). C. pentagona typica
(1903). C. cuspidata

JOHNSTON
(1904). C. epithymum

JONES
571; 1914; (1880). C. curta
1331; (1880). C. indecora neuropetala
1370. C. gronovii vulgivaga
1875; 1915. C. californica breviflora
1918. C. cephalanthi
2316; (1880; 1901). C. salina squamigera
2490; 3712. C. subinclusa
3862. C. veatchii typica
4032; 4116; 5482b; 5653; (1884). C. pentagona calycina
4170; (1884). C. squamata
(1884). C. denticulata

JOOR
(1877). C. pentagona verrucosa
(1891). C. compacta typica

KAMMERER
98. C. planiflora

KARWINSKI
(1827; 1842). C. tinctoria

KEARNEY
52. C. californica brachycalyx
472; 588. C. gronovii vulgivaga
842. C. rostrata
843; 1583. C. pentagona typica
844; 845; 2365. C. compacta typica
(1890). C. glomerata

KEELER
(1889). C. pentagona typica

KELLERMAN
50. C. pentagona calycina
4591; 5576; 5916a. C. corymbosa grandiflora
7567. C. tinctoria kellermaniana
(1890). C. glomerata
(1871). C. cephalanthi

KELLOGG
(1909). C. compacta typica

KELLOGG & HARFORD
779. C. salina major
780. C. pentagona typica

KILBORNE
(1882). C. epilinum

KILLEBREW
(1885). C. pentagona typica

KING
(1894). C. salina major

KIRKWOOD
50. C. decipiens

KNIGHT
(1905). C. gronovii vulgivaga

KNOWLTON
(1895). C. gronovii vulgivaga

KUNTZE
555; 556. C. americana spectabilis
LANGLASSÉ
127. C. americana congesta
438. C. ceratophora
LANGLOIS
237. C. glandulosa
(1879). C. indecora neuropetala
LANSING
2846. C. pentagona typica
3301. C. gronovii vulgivaga
LAPHAM
(1842). C. gronovii vulgivaga
LARRABEE
(1900). C. pentagona verrucosa
LEACH
(1861). C. curta
LEGGETT
(1870). C. coryli
LEHMANN
1682. C. tinctoria
LEIBERG
5266; 5267; 5330. C. californica graciliflora
5268. C. subinclusa
5396. C. indecora neuropetala
5965. C. applanata
LEJOLIS HERB.
(1866). C. gracillima saccharata
LEMMON
(1875). C. californica graciliflora
(1878). C. salina squamigera
(1878). C. subinclusa
(1881). C. indecora neuropetala
..... C. umbellata typica
LEON
7707. C. pentagona calycina
LEON & ECKMAN
4270. C. pentagona calycina
LEONARD
250; (1883). C. curta
LETTERMANN
(1875). C. pentagona typica
(1879); ..... C. compacta typica
LEWIS
224. C. pentagona typica
LIEBMANN
..... C. gracillima saccharata
LINDEN
1994. C. americana spectabilis
..... C. americana congesta
..... C. corymbosa stylosa
LINDHEIMER
10; 1028; (1847). C. glomerata
123; 318; 1029. C. indecora hispidula
124; 474; III 475. C. indecora neuropetala
125; 277. C. cuspidata
126; 664. C. pentagona calycina
127; 473. C. pentagona verrucosa
235?; (1841). C. gronovii calyptrata
472; (1846). C. exaltata
(1847). C. pentagona pubescens
LLOYD
28; 193. C. decipiens
(1888). C. polygonorum
(1890). C. cephalanthi
LLOYD & EARLE
(1900). C. compacta typica
LLOYD & TRACY
124; 128. C. indecora neuropetala
LOWE
(1916). C. epithymum
LUNELL
842; (1908). C. cuspidata
(1907; 1908; 1909; 1912). C. curta
LYALL
(1858–59). C. cephalanthi

MCATEE
1807a. C. compacta typica
MCCALL
(1877). C. gronovii vulgivaga
MCCARTHY
(1885). C. pentagona typica
MCCLATCHIE
(1896). C. salina squamigera
(1892). C. pentagona calycina
MCDONALD
(1885; 1894). C. cephalanthi
(1886; 1887). C. gronovii vulgivaga
(1904). C. pentagona typica
MCDOUGAL
26. C. umbellata reflexa
378. C. pentagona calycina
685. C. indecora neuropetala
(1889). C. gronovii vulgivaga
MCDOUGALL
(1917). C. cephalanthi
MCGREGOR & ABRAMS
36; 700. C. californica graciliflora
MCKINNEY
(1916). C. pentagona calycina
MCMILLAN
(1890). C. glomerata

McMurphy
54. C. salina major
55. C. californica graciliflora
Mackenzie
81. C. umbellata typica
370. C. gronovii latiflora
543. C. cuspidata
2908. C. compacta typica
3797. C. gronovii vulgivaga
4782. C. pentagona typica
Macoun
11852; 23972. C. pentagona calycina
85812; 85818. C. salina squamigera
(1887). C. salina major
Maltby
21. C. salina squamigera
Manning
497; 498. C. subinclusa
Martin
(1889). C. epithymum
Martindale
(1877). C. pentagona typica
..... C. gronovii vulgivaga
Maxon
(1897). C. gronovii vulgivaga
Mayer
(1867). C. gronovii vulgivaga
M. E.
347. C. rugisoceps
Mearns
640; (1887). C. umbellata typica
Merrill
699. C. gronovii vulgivaga
Metcalf
1290. C. leptantha typica
(1903). C. pentagona calycina
Meyer
(1841). C. coryli
Michener & Bioletti
(1891; 1893). C. californica graciliflora
(1891). C. salina major
(1893). C. californica brachycalyx
Milligan
(1907). C. gronovii vulgivaga
Millspaugh & Millspaugh
9029. C. americana congesta
Moffatt
526. C. glomerata
1650. C. gronovii vulgivaga
Mohr
885c; (1876; 1888). C. indecora neuropetala
(1872; 1882; 1893; 1896). C. gronovii vulgivaga
(1874; 1888). C. pentagona typica
(1882). C. polygonorum
(1894). C. cephalanthi
(1896). C. compacta typica
(1899). C. rostrata
Moore
(1918). C. epithymum
Morris
(1897). C. gronovii vulgivaga
Moseley
(1897; 1898). C. polygonorum
(1897). C. cephalanthi
Moser
1832. C. gronovii vulgivaga
Mulford
1078a. C. umbellata typica
(1892). C. curta
Müller
1260. C. corymbosa stylosa
(1853). C. ceratophora
(1853). C. jalapensis
Murdock
2537. C. subinclusa
Nash
759. C. americana spectabilis
2283. C. pentagona typica
Nash & Taylor
1578. C. americana congesta
Nealley
83; 141. C. indecora hispidula
84. C. pentagona pubescens
92. C. glandulosa
94; 126; 278. C. indecora neuropetala
100; 100a. C. umbellata typica
260. C. exaltata
338. C. umbellata reflexa
Nelson
1139; 1210; 4936. C. planiflora
2014. C. corymbosa stylosa
2741 in part; 2768; 9118. C. plattensis
2741 in part; 8576. C. indecora neuropetala
5053. C. curta
Newberry
..... C. subinclusa
Nieuwland
11500. C. gronovii vulgivaga
Norton
358. C. polygonorum
360. C. glomerata

NUTTALL
..... C. coryli
OLDBERG
(1872). C. gronovii vulgivaga
OLNEY
(1872). C. coryli
ORCUTT
1499; (1888). C. californica graciliflora
(1889). C. denticulata
..... C. veatchii typica
OSTERHOUT
4602. C. californica breviflora
OVER
1907. C. pentagona typica
2157. C. indecora neuropetala
2355. C. racemosa chiliana
5131. C. glomerata
OYSTER
5953. C. cuspidata
PAGE
2641. C. compacta typica
PAINTER
745. C. pentagona typica
PALMER
16; 544. C. laptantha palmeri
22; 808; 2737; 2821; 4149; 4757; 8407; 8710. C. gronovii vulgivaga
51. C. gracillima saccharata
52; 141. C. macrocephala
56. C. corymbosa grandiflora
87; 579; 918. C. tinctoria
137; (1879). C. mitraeformis
142; 227; 517; 631½; 641. C. applanata
149. C. racemosa chiliana
173. C. umbellata reflexa
202; 218; 307; 723; 730; 919; 7709; 12914. C. pentagona verrucosa
284; 530; 630. C. indecora neuropetala
331; 341. C. americana congesta
333; 640. C. indecora longisepala
382. C. pentagona calycina
412. C. odontolepis fimbriata
432. C. pentagona typica
411; 471; 500; 501; 506; 511; 916. C. umbellata typica
605. C. glandulosa
631. C. jalapensis
818; 3069; 3129; 3861. C. glomerata
948. C. deltoidea
949. C. gracillima subtilis
1209. C. umbellata dubia
1292; 2737. C. gronovii latiflora
2392d; 2761. C. californica graciliflora
3197; 3835. C. coryli
6684. C. cuspidata
6840; 8476. C. compacta typica
(1869). C. erosa
PAMMEL
(1886). C. gronovii vulgivaga
(1888); ..... C. coryli
PAMMEL & BALL
79. C. glomerata
PARISH
538a; 4130; 5524. C. californica papillosa
539; 3958; 5533. C. subinclusa
2174; 6012. C. salina squamigera
2281. C. salina major
2436; 3230; 3231; 3236. C. denticulata
5905; 5532. C. indecora neuropetala
(1898); ..... C. glandulosa
PARKER
(1866). C. pentagona typica
PARLIN
875. C. epithymum
PARRY
205. C. denticulata
206. C. salina squamigera
273. C. cuspidata
500. C. applanata
(1850). C. californica graciliflora
(1852). C. squamata
PARRY & PALMER
631. C. tinctoria
(1877). C. corymbosa stylosa
PATTERSON
10430; (1872); ..... C. cephalanthi
..... C. glomerata
..... C. pentagona typica
PAYSON
588. C. pentagona calycina
PEASE
..... C. cephalanthi
PEIRSON
150; 261. C. subinclusa
150a. C. californica graciliflora
PEPOON
190; 191; 450; 837; 892. C. gronovii vulgivaga
300; 936. C. glomerata
PERRINE
(1896). C. curta

PETERSEN
(1908). C. indecora neuropetala
(1909). C. curta
PINEO
..... C. salina major
PIPER
715. C. salina major
(1898). C. epithymum
PITTIER
497. C. umbellata typica
PLANK
(1891). C. indecora neuropetala
(1895). C. umbellata typica
POITEAU
(1802; 1845). C. americana spectabilis
..... C. europaea
POL
(1888). C. coryli
POLLARD
239. C. cephalanthi
1280. C. glomerata
(1894). C. gronovii vulgivaga
POLLARD & MAXON
341. C. harperi
POLLARD & PALMER
393. C. americana spectabilis
POLLOCK
..... C. gronovii vulgivaga
PORTER
(1863). C. epilinum
(1863). C. polygonorum
(1864; 1879; 1890; 1895). C. cephalanthi
(1869). C. gronovii vulgivaga
(1873). C. indecora neuropetala
(1873). C. curta
(1879) C. gronovii latiflora
POUND
(1889). C. gronovii vulgivaga
PRICE
(1897). C. compacta typica
(1898). C. pentagona typica
(1898). C. polygonorum
PRINGLE
105. C. desmouliniana
144; 3111; 13797; (1891). C. pentagona calycina
145. C. subinclusa
291; 1342. C. jalapensis
783; 6297. C. umbellata typica
784. C. applanata
785. C. squamata
2472. C. pringlei
4330. C. mitraeformis
4331; 11306. C. corymbosa grandiflora
4529. C. tinctoria
4967. C. rugosiceps
5349. C. chapalana
6189; 8716. C. gracillima subtilis
6574. C. corymbosa stylosa
6575; 7179. C. potosina globifera
8514. C. epithymum
(1880). C. epilinum
(1881; 1884). C. indecora neuropetala
(1884). C. tuberculata
PROUT
(1840). C. gronovii vulgivaga
PURPUS
3553; 5708. C. tinctoria
4563; 6343. C. indecora neuropetala
4873. C. decipiens
4971; 5036. C. choisiana
4972; 5444. C. purpusii
5678. C. salina acuminata
5709. C. potosina globifera
5730. C. applanata
5745; 7564; 7775. C. corymbosa stylosa
8175. C. pringlei
8274. C. umbellata typica
..... C. indecora bifida
RATTAN
4d. C. pentagona calycina
293. C. subinclusa
RAVENEL
(1869); ..... C. pentagona typica
(1874). C. compacta typica
REDFIELD
5652; 5845; 5851; (1874). C. compacta typica
5853; 5854. C. gronovii vulgivaga
5859. C. subinclusa
REED
2372. C. californica papillosa
(1911). C. californica brachycalyx
REMY
(1855). C. salina squamigera
(1855). C. subinclusa
REPPERT
(1895). C. cuspidata
REVERCHON
663; 2552; (1875; 1880). C. exaltata
664; 2194; 3202. C. cuspidata
1686. C. glomerata

3201; 3883. C. compacta typica
(1875). C. indecora longisepala
(1878). C. glandulosa
(1878). C. pentagona verrucosa
(1878). C. cephalanthi
(1880). C. pentagona calycina
..... C. gronovii latiflora

REYNOLDS
(1872). C. pentagona typica

RICH
(1896). C. pentagona typica

RICKER
469; 1396; 1397. C. gronovii vulgivaga

RICKSECKER
93; 313; 313a. C. americana spectabilis

RIEHL
15; 16. C. glomerata
(1843). C. gronovii latiflora
(1848). C. pentagona typica

RIES
(1893). C. cuspidata

ROLFS
508; 510. C. compacta typica

ROSE
2445. C. applanata
11887. C. indecora neuropetala
12074. C. denticulata
16206. C. californica breviflora

ROSE & FITCH
17027. C. indecora neuropetala

ROSE, FITCH & RUSSELL
3279; 3604; 3608; 3763; 3853. C. americana spectabilis
3691. C. americana congesta

ROSE & HAY
5866. C. applanata
6170. C. mitraeformis

ROSE & PAINTER
7473. C. tinctoria

ROSE, PAINTER & ROSE
9650. C. potosina typica
9887; 9888; 10275. C. applanata

ROSE & ROSE
11150. C. tinctoria
11215. C. potosina globifera
11413. C. applanata

ROSE, STANDLEY & RUSSELL
12477. C. indecora neuropetala
13727. C. americana congesta
13727a; 13804. C. gracillima subtilis
14329. C. corymbosa grandiflora
14929. C. leptantha typica

ROTHROCK
101. C. salina squamigera
311; 708. C. pentagona calycina

ROWLEE
(1906). C. gronovii vulgivaga

RUGEL
400; (1843). C. glandulosa
400a; 400b; (1843). C. pentagona typica
(1841); ..... C. rostrata

RUSBY
85; 245; 295; (1880). C. pentagona calycina
129. C. umbellata typica
295. C. potosina globifera
(1909). C. californica graciliflora

RUSSELL
(1897). C. cuspidata
(1897). C. pentagona typica
..... C. gronovii latiflora

RUTH
8. C. gronovii vulgivaga
159; 188. C. indecora hispidula
169; 477; 492. C. pentagona typica
317. C. cuspidata
493; (1893). C. harperi
502. C. pentagona verrucosa
(1893; 1895). C. compacta typica
(1893). C. pentagona calycina

RYDBERG
264. C. pentagona calycina
1634; 1694; 3700; (1890). C. indecora neuropetala
1639. C. cuspidata
1688; 8179; 8183. C. coryli
8073. C. gronovii vulgivaga

RYDBERG & GARRETT
8541. C. planiflora
9918; 10013; 10014. C. pentagona calycina

SANDBERG
841; (1890). C. gronovii vulgivaga

SANDBERG & LEIBERG
495. C. californica breviflora

SCAMMON
1. C. coryli

SCHAFFNER
377; 781. C. tinctoria
378; 780. C. potosina globifera
379; 779. C. potosina typica
..... C. macrocephala
..... C. polyanthemos

SCHEIDE
152. C. jalapensis

SCHNECK
(1877). C. glomerata
(1880; 1881). C. coryli
(1879; 1880; 1897; 1905). C. polygonorum
(1880). C. cephalanthi
(1887). C. compacta typica
(1906). C. pentagona typica
..... C. gronovii vulgivaga

SCHOCKLEY
443. C. denticulata

SCHOTT
(1851). C. glandulosa
..... C. cuspidata
..... C. umbellata typica

SCHRENK
(1890). C. epilinum
(1892). C. gronovii vulgivaga

SCHUEBURT
(1893). C. curta

SCHUETTE
95–11–7. C. polygonorum
(1894). C. cephalanthi

SCHURTZ
(1907). C. epithymum

SCOTT
(1886). C. gronovii vulgivaga

SEAMAN
..... C. compacta typica

SEARS
(1916). C. polygonorum

SEYMOUR
20. C. gronovii vulgivaga

SHAFER
31. C. americana spectabilis
2635. C. indecora hispidula

SHANNON
127. C. glomerata

SHEAR
(1891). C. gronovii vulgivaga

SHELDARD
(1892). C. cephalanthi

SHELDON
21; (1891). C. pentagona typica
134. C. indecora hispidula
263; (1884). C. glomerata
8715. C. californica breviflora
(1892). C. coryli
(1892). C. indecora neuropetala

SHERFF
1755; (1911). C. glomerata
1813; 1979. C. gronovii vulgivaga
1896; (1911). C. cephalanthi
(1911). C. coryli

SHORT
(1840). C. gronovii vulgivaga
(1843). C. gronovii latiflora

SHREVE
381. C. gronovii vulgivaga

SHULL
112; 189; 289; 368. C. gronovii vulgivaga
204; 367. C. compacta typica
393. C. polygonorum

SHUTTLEWORTH
(1843). C. gronovii vulgivaga

SIEBER
91. C. americana congesta

SIMPSON
68; (1889). C. indecora neuropetala
361. C. umbellata typica
380. C. gronovii vulgivaga

SINTENSIS
3239. C. americana spectabilis
3851. C. indecora neuropetala

SKEELS & SHADDICK
(1900). C. coryli

SKINNER
200. C. pentagona typica

SMALL
(1888). C. cephalanthi
(1890; 1894). C. gronovii vulgivaga
(1893). C. pentagona typica
(1893; 1894). C. compacta typica

SMART
345. C. indecora neuropetala

SMITH
204. C. mitraeformis
406. C. lacerata
1831. C. planiflora
1912. C. corymbosa grandiflora
(1897). C. indecora hispidula

SMYTH
80a; 80c; 80e; 80f; 80g; 80i; 80k. C. cuspidata
250b; 250c. C. glomerata

SONES
79. C. californica brachycalyx

SPENCER
(1919). C. glomerata

STANDLEY
426; 6370; (1906). C. squamata
5372. C. rostrata
6958. C pentagona calycina
7849. C. umbellata typica
8058. C. planiflora
8456; 9156; (1905). C. glomerata
8980. C. pentagona typica
9502; 9848; 9902. C. gronovii vulgivaga
9700. C. cuspidata
9937. C. coryli

STANDLEY & BULLMAN
12271. C. gronovii vulgivaga

STANFIELD
(1898). C. pentagona calycina

STEARNS
205; C. applanata
455. C. squamata

STEELE
93; (1898; 1906; 1912). C. gronovii vulgivaga
155. C. pentagona typica
(1896; 1902; 1904). C. compacta typica
(1900). C. polygonorum
(1906). C. rostrata

STEVENS
1000. C. indecora hispidula
2641. C. compacta typica
(1853). C. salina major
(1895). C. gronovii vulgivaga
..... C. glomerata
..... C. cephalanthi

STUDLEY
4d. C. indecora neuropetala

STURTEVANT
(1862; 1888). C. gronovii vulgivaga
(1890). C. cephalanthi

SUKSDORF
1487. C. salina acuminata
2852. C. plattensis
(1883). C. cephalanthi

TAINTURIER
..... C. glandulosa

TATNALL
(1863). C. epilinum
(1884). C. pentagona typica
..... C. polygonorum

TAYLOR
2606. C. gronovii latiflora
(1892). C. gronovii vulgivaga

THACHER
34. C. subinclusa

THAXTER
(1887). C. pentagona typica

THOMPSON
159. C. indecora neuropetala
(1898). C. cuspidata

THORNBER
32; 87; 133. C. indecora neuropetala
2462; 7516; (1901) C. salina squamigera
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THE LARVAE OF THE COCCINELLIDAE

WITH SIX PLATES

BY

J. HOWARD GAGE

Contributions from the
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No. 62.

THESIS

SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE IN ENTOMOLOGY IN THE GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS

1919

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INTRODUCTION

The adults of this family are known to most persons as lady-bugs or ladybirds. Their distinctive characteristics are the apparently three-segmented tarsi and the broad hatchet-shaped distal segment of the maxillary palpi. Other characteristics are: the eleven segmented antennae, in which the distal segments are commonly modified to form a more or less distinct club-shaped enlargement; the insertion of the antennae near the mesal margin of the compound eyes; the ventral direction of the mouth; the retraction of the head into the small transverse prothorax; the transverse front coxae; the closed coxal cavities, except in Coccidula; the convex elytra; and the abdomen consisting of five to seven exposed ventral segments.

Le Baron has said, in speaking of this family, that "The Coccinellidae occupy a remarkably anomalous and isolated position. Whilst having the rounded form of the plant beetles, the clavate antennae of the scavangers, and the dilated palpi of the fungus beetles, they agree in food and habits with none of these, but resemble in their predaceous habits the ground beetles and the soft-winged carnivora, all of which have their bodies more or less elongated, their tarsi five-jointed, their antennae filiform, and their palpi slender or moderately dilated."

The larvae of the Coccinellidae, though they may be known to many people, are not as a rule associated with the adult coccinellids or lady-bugs. The most distinctive characteristics of these larvae are: their porcupine-like appearance; elongated body which is usually striped or mottled with red, black, white or yellow areas; small three-segmented antennae; powerful mandibles; and the habit of being continually on the move. From the systematist's point of view these larvae do not show any unusual characteristics such as Le Baron has noted for the adults, for they resemble in most respects the distinctly predaceous types of coleopterous larvae. This is true even of the Epilachninae, which are phytophagous. With the exception of this subfamily the Coccinellidae are all more or less predaceous in their adult stages, and almost entirely so in their larval stages.

The purpose of this investigation is to study the morphology of coccinellid larvae and to arrange tables for the identification and classification of a few of the more common species. The work has been limited to those genera and species which have in the main been found in or reported from Illinois. Specimens were collected and bred during the autumn of 1918, and others were obtained from the collections of Dr. A. D. MacGillivray, the University of Illinois, the Illinois State Natural History Survey, and a specimen of *Brachyacantha ursina* received from Cornell University.

The investigation of the immature stages of insects was to a great extent neglected by entomologists until about the beginning of the twentieth century. There has been some previous work done, however, upon the immature stages of the Coccinellidae. The works of L. Ganglbauer (1899), Dimmock (1906), Palmer (1914), and Böving (1917) are valuable to one pursuing a study of the immature stages of these beetles.

I am greatly indebted to Dr. A. D. MacGillivray, under whose supervision this work was carried on, for the interest he has shown at all times, for the use of specimens from his collection, and for the privilege of using the morphological nomenclature which he has devised. I am likewise indebted to Professor S. A. Forbes for the use of material belonging to the Illinois State Natural History Survey, and to Professor J. G. Needham for the loan of material from Cornell University.

MORPHOLOGY

This discussion of the general comparative morphology of coccinellid larvae is based for the most part upon a study of *Chilocorus bivulnerus*. This species represents the most generalized condition of the carnivorous coccinellids that I have studied. A still more generalized condition occurs, however, in the subfamily Epilachninae, the members of which are for the most part entirely phytophagous.

HEAD

The heads of coccinellid larvae are symmetrical and the general outline is circular or nearly so, except in the genus Microweisea in which it is oval or oblong. In Chilocorus and Epilachna the mouth is directed ventrad; while in all of the genera of the Coccinellini, Hyperaspini, and Microweiseini it is directed caudo-ventrad. The greatest departure from the generalized condition is found in Scymnus. In this genus the mouth is directed cephalad. For the sake of convenience the head will be considered under two divisions; first, the fixed parts; second, the movable parts.

Fixed Parts of the Head

The fixed parts of the head consist of an external and an internal skeleton. The external skeleton is composed of the fused front and postclypeus, preclypeus, veterx, labrum, and gula. The boundaries of these sclerites are marked by distinct furrows or sutures. The internal skeleton is made up of the floor-like tentorium, which in the Coccinellidae consists of three parts.

In the head capsule of *C. bivulnerus* the epicranial suture (Fig. 6, *es*) is present on the meson. It extends from the occipital foramen (Fig. 17, *of*) to a point on the cephalic aspect about one-third the distance from the occipital foramen to a line drawn through the antennal fossae. This part of the epicranial suture is the epicranial stem (Fig. 6, *es*). The epicranial stem bifurcates at its ventral end and the two epicranial arms (Fig. 6, *ea*) extend latero-ventrad a short distance, then make a broad curve and extend ventro-mesad on each side to a point where they become much thickened. Each thickening is a pretentorina (Fig. 6, *pt*) and marks the point of invagination of the pretentorium. The epicranial arms curve broadly laterad and ventrad from each pretentorina to a point dorsomesad of an antennal fossa where they become obsolete. The three sclerites included within or ventrad of the fork of the epicranial stem are the fused front and postclypeus (Fig. 6, *fc*) and the labrum (Fig. 6, *l*). There is an indistinct furrow which marks the position of the clypeal

suture (Fig. 6, *cs*) on each lateral margin of the head. There is a distinct precoila (Fig. 6, *pcl*), in which a preartis articulates, located on each side of the postclypeus meso-ventrad of the antennal fossa at the point of origin of the clypeal suture. The vertex occupies all of the dorsal and lateral parts of the head capsule not included within the fork of the epicranial suture (Fig. 6, *v*). There are six ocelli (Fig. 6, *oc*), in two groups of three. Each group is situated on the lateral margin of the vertex dorsad and laterad of the lateral end of an epicranial arm. The antennal fossae are located ventrad of the ocelli on the dorso-lateral margin of the vertex. The large somewhat oval opening in the caudal aspect of the head is the occipital foramen (Fig. 17, *of*).

A primitive type of epicranial suture is found in the adults of Periplaneta and the larvae of Corydalis. The condition of the epicranial suture in *C. bivulnerus* is very similar to that of these primitive forms, except that the epicranial stem is not so long in proportion to the length of the epicranial arms and that a portion of each arm is wanting near the antennal fossae. This suture in Epilachna (Fig. 4, *es*) very closely resembles that of *C. bivulnerus*, but the epicranial stem is much longer and extends almost one-half the distance from the occipital foramen to a line drawn through the antennal fossae. In Megilla the epicranial suture (Fig. 7, *es*) is present but very short, not extending more than one-fifth the distance from the occipital foramen to a line drawn through the antennal fossae; while in Adalia, Anatis, Hippodamia, Coccinella, and Microweisea the epicranial stem is not present and the epicranial arms diverge immediately from the occipital foramen. In the adult larval stage of Hyperaspis the epicranial suture is wanting, but it is present in the first instar. The epicranial stem is absent in the second instar, but the epicranial arms are present; while in the later larval instars the entire epicranial suture is wanting. The adult larvae of Scymnus (Fig. 14) also lack an epicranial suture; no observations were made on the conditions present in very young larvae.

The epicranial arms are present in most coccinellid larvae, but are absent in the adult larvae of Scymnus and Hyperaspis. In *C. bivulnerus* the epicranial arms extend ventro-laterad from their point of origin to a point dorso-mesad of the antennal fossae. In Epilachna the epicranial arms extend ventrad of the antennal fossae, but do not extend as far laterad. In Chilocorus and Epilachna the epicranial arms are not widely divergent, but in all of the genera of the Coccinellini they diverge widely and become obsolete slightly ventrad of the antennal fossae. In the first larval instar of Hyperaspis they diverge immediately upon the dorsocephalic aspect of the head, the epicranial stem being very short, and they extend laterad almost parallel with the caudal margin of the head, make an abrupt turn and extend laterad and ventrad to their point of obsolescence. In Microweisea (Fig. 13) the epicranial arms diverge gradually

latero-ventrad and become obsolete dorsad of the antennal fossae. Due to the extreme length of the head in this genus, these arms are very long. In Scymnus the epicranial arms are entirely wanting.

The two proximal unpaired sclerites between the arms of the epicranial suture in Corydalis are the fused front and postclypeus. These areas are separated from each other in the more generalized forms by the fronto-clypeal suture; in the specialized forms, however, they may become completely fused. In such cases the fronto-clypeal suture is absent, but portions of it may be indicated by a furrow on each lateral portion of the head. These portions extend mesad from near the precoila. In *C. bivulnerus* and all coccinellid larvae the front and post-clypeus (Fig. 6, *fc*) are completely fused and the fronto-clypeal suture is wanting. The clypeal suture (Fig. 6, *cs*) is indicated by an indistinct furrow extending mesad from the precoila (Figs. 5 and 6, *pcl*). The area ventrad of this furrow in the preclypeus (Fig. 6, *pc*) and the area dorsad of it is the fused front and postclypeus (Fig. 6, *fc*). In Epilachna (Fig. 4) the front and postclypeus are entirely separated from the preclypeus by the complete clypeal suture; while in all of the other genera of the family that were studied the condition of the clypeal suture is approximately that found in Chilocorus.

The labrum of *C. bivulnerus* is the distinct, slightly chitinized, shield-like sclerite attached to the ventral margin of the preclypeus (Fig. 6, *l*). The ventral margin of the labrum may be slightly emarginate and usually bears four or six medium-sized setae. In general the structure of the labrum in all of the coccinellids studied approximates very closely the condition found in the labrum of *C. bivulnerus*. Its general shape, however, varies in the different genera of the family. In the genus Epilachna the labrum varies most widely from the Chilocorus type. In this genus it is broadly transverse and widely but shallowly emarginate on the ventral margin.

The vertex of *C. bivulnerus* (Fig. 6, *v*) consists of the paired continuous areas on the cephalic and dorsal aspect of the head. In Chilocorus, Epilachna, and Megilla the epicranial stem is present and marks the line of separation of the two halves of the vertex; in Hippodamia, Coccinella, Anatis, Adalia, and Microweisea the epicranial arms alone are present and the two halves of the vertex do not meet on the meson, but a portion of the front extends between them to the occipital foramen. In Hyperaspis and Scymnus the epicranial suture is absent and the front, postclypeus, and vertex are fused. The vertex is continuous on its lateral and caudo-lateral margins with the genae (Fig. 5, *ge*), the region of the vertex ventrad and mesad of the ocelli and the antennal fossae. The size, shape, and extent of the vertex is dependent upon the location and extent of the epicranial suture.

In the head of Corydalis caudad of the antennae there is a distinct ocularium which bears five or six ocelli. This indicates the position of the developing compound eyes. In *C. bivulnerus* the ocelli (Figs. 5 and 6, *oc*) are placed three on each lateral aspect of the head dorsad of the antennal fossae. They are usually arranged in the form of a triangle. These ocelli are undoubtedly the homologues of the ocelli of Corydalis and represent the developing compound eye of the adult. The arrangement, number, and position of the ocelli is fairly constant in all of the genera of the family. There is only one exception worthy of note; the region bearing the ocelli in Scymnus is darkened and slightly chitinized. Two of the ocelli are equal in size, while the third is almost twice as large as either of the others.

In generalized insects the gula is present as a distinct chitinized sclerite extending cephalad from the occipital foramen to the articulation of the maxillae and submentum. It is bounded on its lateral margins by the postgenae. In all of the larvae of the Coccinellidae the gula (Fig. 17, *g*) is present as a more or less membraneous, rectangular, glabrous area caudad and dorsad of the submentum.

The internal skeleton of the head of insects is formed by invaginations. It serves undoubtedly to make the head more rigid, to support the soft and delicate parts, and as a place for the attachment of muscles. The entire internal skeleton of the head is known as the tentorium (Fig. 47). It consists of two or three pairs of arms that have been invaginated from the external skeleton. In the more primitive forms there may be only two pairs. In all of the larvae of the Coccinellidae there are three distinct pairs of arms.

The pretentoria, also known as the anterior arms of the tentorium (Fig. 47, *prt*), are invaginated on the dorsal aspect of the head near the point where the epicranial arms turn abruptly laterad.

The supratentoria, sometimes called the dorsal arms of the tentorium (Fig. 47, *sup*), are invaginated mesad of the antennal fossae and are well developed in the larvae of the Coccinellidae.

The metatentoria or the posterior arms of the tentorium (Fig. 47, *met*) are invaginated on the ventral aspect of the head near the articulations of the maxillae.

In many insects the occipital foramen is divided into two parts by a distinct bridge. This bridge is the corpotentorium. In coccinellid larvae the corpotentorium is not united to form a complete bridge, but the mesal boundaries of the two lobes which ordinarily fuse to form the corpotentorium (Fig. 47, *cp*) approximate each other very closely on the ventral aspect of the head and are located much nearer the mouth than the occipital foramen. The metatentoria extend dorsad from their point of invagination along the gular sutures toward the occipital foramen and form important landmarks for the identification of the gula. When they

reach the occipital foramen, they diverge laterad and form a ring around the entire opening.

The small bridge-like structure about one-half way between the lobes of the corpotentorium and the occipital foramen is the laminitentorium (Fig. 47, *lt*). It is formed by the fusion of the ends of the pretentoria, supratentoria, and metatentoria.

The small pit on the ectal surface of the dorso-cephalic aspect of the head where each pretentorium is invaginated is a pretentorina (Fig. 4, *pt*). The point on the ectal surface of the head marking the place of invagination of each supratentorium is a supratentorina (Fig. 6, *supt*). It is not present as a pit in coccinellid larvae. The metatentorina is the point of invagination of each metatentorium on the caudo-ventral aspect of the head. The metatentorinae are not indicated by a pit or thickening.

Movable Parts of the Head

The form, structure, and arrangement of the movable parts of the head of coccinellid larvae are readily homologized with the movable parts of the head of generalized insects, such as Periplaneta or the larvae of Corydalis or the adults of the Carabidae. The movable parts consist of the antennae, mandibles, maxillae, and labium.

The antennae of *C. bivulnerus* (Fig. 36) are about as long as wide, slightly conical, and composed of three segments. The scape (Fig. 36, *sc*) is cylindrical, wider than long, slightly chitinized, and bears a few fine setae. The scape is attached to the heavily chitinized antennaria which bounds the periphery of the antennal fossae (Fig. 36, *ant*) by a delicate membrane, the antacoria (Fig. 36, *antc*). The pedicel or second segment (Fig. 36, *pd*) is distinctly smaller than the scape, about as wide as long, and bears a distinct long seta on its mesal surface near the distal end. It also bears a small number of fine setae. The flagellum, the small mound-like segment on the distal end of the pedicel (Fig. 36, *fl*), usually appears to be a part of the pedicel, but careful examination shows it to be distinctly separated from it. The flagellum usually bears three peg-like setae which are probably tactile organs (Fig. 36, *ts*) and four small oval openings which are probably sensoria (Fig. 36, *se*).

The antennae of Epilachna (Fig. 35) are about three times as long as wide; the greater part of the elongation is found in the pedicel. In this segment the peg-like seta at the distal end is clearly a part of the pedicel and does not appear as a part of the flagellum as in the other genera of the family. In all of the genera of the tribe Coccinellini and in the genus Microweisea the antennae are less than twice as long as wide and the antacoriae are protuberant and might easily be mistaken for the first antennal segment. The condition of the remaining parts is similar to that of Chilocorus. In Hyperaspis the antacoria (Fig. 38, *antc*) is more pro-

tuberant than in the Coccinellini, the flagellum is more mound-like, and one of the three apical setae is much larger than the other two. Scymnus (Fig. 39) presents a type of antennae that shows a wide variation from the type found in the other genera of the family. The antenna of this genus is wider than long, only slightly chitinized, scarcely elevated, and conical. The antacoria (Fig. 39, *antc*) is narrow; the scape (Fig. 39, *sc*) is about three times as wide as long; the pedicel (Fig. 39, *pd*) is about twice as wide as long, its distal end much narrower than the proximal; and the flagellum (Fig. 39, *fl*) is more or less mound-like and about twice as wide as long.

All of the coccinellid larvae examined have well-developed mandibles. They may be of a crushing type, that is with many dentes as in Epilachna, or they may be of a piercing type, that is with one or two dentes as in all of the members of the subfamily Coccinellinae. Within the family there are all stages of variation between these two extremes. The type of mandible found in such generalized genera as Periplaneta or Corydalis is that with many dentes. This tends to show that in these forms the mandible is a crushing organ primarily and not for piercing as appears to be the case in the specialized coccinellid larvae.

The mandible of *C. bivulnerus* (Figs. 40, 41) is of moderate size, heavily chitinized, somewhat triangular in outline, thick and heavy at the proximal end, and tapering to a bidentate distal point. The proximo-mesal margin of each mandible is provided with a distinct wedge-shaped mola (Fig. 41, *mo*) and the proximo-lateral margin with a stout spine-like seta. On the cephalo-mesal margin of each there is a preartis (Figs. 42, 41, *ps*) which articulates in a precoila (Fig. 5, *pcl*); on the caudo-mesal margin there is a postartis (Fig. 41, *poa*) which articulates in a postcoila. The mandibles of Chilocorus are intermediate in form between the two extreme types. The majority of the species studied have mandibles similar to those of Chilocorus and tend to show an evolution from the multidentate type found in Epilachna, which are entirely phytophagous, to the unidentate type found in Hyperaspis, Microweisea, and Scymnus, which are entirely carnivorous. In all of the genera studied the mola is present, but it is much reduced, is almost indistinguishable in Epilachna (Fig. 42, *mo*) and shows the extreme condition of its reduction in Microweisea. The mandibles of all coccinellid larvae are connected with the head capsule cephalad and ventrad of the antennal fossae by a small and distinct membrane. This membrane is the mandacoria (Fig. 5, *mco*). The extensor muscles are attached to the lateral margin of the mandible between the preartis and the postartis, while the retractor muscles are attached near the mesal portion of the mandible.

The maxillae of the Coccinellidae show a greater degree of departure from the primitive type than any other of the movable parts. They resemble in general form the maxillae of Periplaneta and the larvae of

Corydalis, but show a more striking resemblance to the conditions found in the maxillae of carabid larvae. Though the coccinellid maxillae are similar in form to those of Periplaneta or to those of the larvae of Corydalis, they also show a great difference in structure and are much more specialized than those of carabid larvae. In order to homologize the parts of the maxilla, it was necessary to trace the development of this appendage from the more generalized to the more specialized condition. In the tracing of this development maxillae of the larvae of Carabidae, Lachnosterna, Elateridae, and Curculionidae were found most useful.

Each maxilla of *C. bivulnerus* is moderately large, slightly chitinized, and consists of the following parts: a fused cardo and stipes, a palpifer, a maxillary palpus, and a galea. The lacinia is apparently wanting.

In the primitive type of coleopterous larvae the cardines are composed of two sclerites; the subcardo, which articulates with the postcoila and a second sclerite, the alacardo, which lies between the subcardo and stipes. This condition is found in the larvae of Pterostichus and Lachnosterna; while in the larvae of a curculionid beetle, Phytonomus, the subcardo and alacardo are fused. A similar condition is found in the larvae of the Elateridae. In the Coccinellidae the subcardo and alacardo are not only fused to form the cardo, but the cardo and stipes are fused and the extent of the cardo is only indicated by small and in many cases indistinct notches along the sides of the fused cardo and stipes. This indication of the suture between the cardo and stipes is found in the maxillae of all of the larvae studied and there is but little variation shown. It will be seen from the above that the stipes and cardo must be discussed as one sclerite. This sclerite (Fig. 18, *ss+ca*) occupies the area at the proximal end of the maxilla cephalad or ventrad of the gula. Its form in *C. bivulnerus* is that of a rectangle. It is about as wide as long, slightly setaceous, and chitinized. This general form of the stipes and cardo is found in all of the genera studied except Microweisea, Scymnus, and Hyperaspis. In these genera the stipes and cardo are narrow and elongated. In Microweisea and Hyperaspis the proximal end is curved laterad. This curved portion represents the cardo and the remaining part of the sclerite is the stipes.

The palpifer is present as a distinct shoulder-like area (Fig. 18, *pf*) near the distal margin of the fused stipes and cardo. Its form and position are generally constant in all of the genera studied. This area bears at its distal extremity the three-segmented maxillary palpus. The maxillary palpus (Fig. 18, *mxpl*) is well developed in all of the genera. In *C. bivulnerus* they are stout and slightly chitinized. The first segment is cylindrical, wider than long, and usually with one or two small setae. The second segment is longer than wide and with one or two large setae. The third segment is conical, about one-half as long as wide with two or three setae and with a group of sensory organs at its distal end. The maxillary palpus

in Epilachna (Fig. 16, *mxpl*) is much elongated, the proximal segment is nearly twice as long as wide, the second segment more than twice as long as wide, and the conical third segment nearly three times as long as wide. In all of the other genera the maxillary palpus resembles that of *C. bivulnerus* and the distal segment of each bears a group of peg-like organs, tactile setae.

The galea (Fig. 18, *ga*) in *C. bivulnerus* is the broad triangular area distad of the palpifer. Its shape and structure is more or less constant throughout the family, the most notable exception being found in Hyperaspis (Fig. 27, *ga*). In this genus the galea is rounded and appears to be more or less sponge-like and bears a few setae. In Epilachna (Fig. 16, *ga*) the distal margin of the galea is densely setaceous, while in all of the other genera of the family it bears only a few setae. There is a peg-like structure on the galea that bears a striking resemblance to the distagalea; this is nothing more than a tactile seta and cannot be interpreted as a distagalea.

The mesal margins of the maxillae and the lateral margins of the labium are connected in all of the genera by a distinct membrane, the labiacoria (Fig. 18, *lic*). The lateral margins of the maxillae and the mandibles are connected by a similar membrane, the maxacoria (Fig. 18, *mxc*). An extension of the maxacoria connects the stipes and cardo of each side to a postgena.

The labium of coccinellid larvae differs considerably from that found in the more primitive forms, as the larvae of Corydalis and the adults of Periplaneta. Many of the parts seem to be lacking. The type of labium found in the more generalized coleopterous larvae shows but little resemblance to the coccinellid labium. By a study of the labia of the primitive forms named and of the more generalized Coleoptera, one is able to homologize the parts.

The labium of *C. bivulnerus* is the more or less membraneous area cephalad and ventrad of the gula and between the maxillae. It appears to be made up of two parts, the submentum (Fig. 18, *su*) and the ligula (Fig. 18, *lig.*). The mentum is indistinguishable or fused with the ligula. The submentum (Fig. 18, *su*) is the large proximal portion. It is membraneous, more or less rectangular, usually with four setae, two large ones which decussate, and two smaller ones. In Anatis, Megilla, Coccinella, and Hippodamia there may be many setae on the submentum, the number varying from four in *Hippodamia convergens* to eighteen in Anatis. The submentum is not clearly or distinctly separated from the ligula in *C. bivulnerus* but there is a distinct division between the two in Epilachna (Fig. 16), while in Hyperaspis (Fig. 27) the division between the ligula and submentum is entirely obsolete. In all of the other genera studied the condition of this division approximates that found in Chilocorus. The

ligula is the distal portion of the labium. In *C. bivulnerus* it is composed of the fused stipulae, glossae, and paraglossae. Near the ventro-lateral margin there is a distinct shoulder-like swelling, the palpiger (Fig. 18, *pg*), which bears a two-segmented labial palpus (Fig. 18, *lipl*). There is a heavy, semicircular, chitinous band (Fig. 18, *cb*) that surrounds each palpiger which probably serves to increase its rigidity. Each labial palpus consists of two segments. The proximal segment is short, as wide as long; while the distal segment is conical and bears a group of tactile setae at its distal end. The ligula also bears four to six moderately large setae. The type of ligula found in *C. bivulnerus* is remarkably constant within the family, the only notable variation being found in Hyperaspis, where the labial palpi have been reduced to a single dome-like segment which bears a few tactile setae (Fig. 27, *lipl*).

THORAX

That part of the body caudad of the head consists of thirteen segments. The dorsal surface of the segments is convex and the ventral surface concave or flattened. They may be provided with scoli, senti, parascoli, strumae, verrucae, or chalazae and setae. The variation in the type of armature will be taken up later. The first three segments constitute the thorax and the remainder the abdomen. In all of the genera of the family the thoracic segments are distinctly separated from each other by a deep coria, more distinct on the ventral than on dorsal surfaces.

Prothorax

The prothorax of *C. bivulnerus* (Figs. 1, 2 and 3, *prth*) is about two-thirds as long as the mesothorax and metathorax combined. The same is true of Epilachna, Microweisea, Scymnus, and Hyperaspis; while in all of the genera of the Coccinellini the prothorax is about one-half as long as the other thoracic segments together.

The tergum is usually convex and oval in outline when viewed from above (Figs. 1 and 2, *t*). In *C. bivulnerus* the greater part of the dorsum is covered with a dark heavily chitinized dorsal shield from which the cone-like senti project. This shield is formed by the fusion of pinacula and its surface bears numerous fine setae. The dorsal shield, when viewed from above, appears to be rectangular in outline and is divided into two parts by a slender white line extending along the dorso-meson. The senti are arranged in three distinct groups, a cephalic group of six placed in a transverse row near the cephalic margin, a lateral group of one placed near the middle of each lateral margin, and a caudal group of one placed near the middle of each half upon the caudal margin. In Epilachna the dorsal shield does not cover such a large portion of the dorsum. It is more or less oval in outline and bears only the cephalic row of four scoli. Its sur-

face is also covered with short fine setae. In all of the genera of the Coccinellini the dorsal shield is large and covers the greater part of the dorsal aspect. It is not so heavily chitinized as in Chilocorus and is divided longitudinally into four plates. Two of these are adjacent on the dorsomeson and each bears three or more large chalazae and many small setae. The lateral plates are smaller than the mesal and bear a fringe of large chalazae on their lateral and cephalic margins. In Microweisea and Scymnus the dorsal shield is only indicated and very slightly chitinized. It appears to extend over the larger part of the dorsum and bears several large black setae. These are arranged in three transverse rows, a row on the cephalic and caudal margins and another midway between them. In Hyperaspis the dorsal shield is wanting and the tergum is only slightly chitinized. It is traversed by three rows of prominent black setae arranged as in Scymnus and Microweisea. There are in addition to these larger setae, many smaller and inconspicuous ones.

The pleural area in *C. bivulnerus* is the more or less reduced area ventrad of the dorsal shield (Fig. 2, *prpl*). It extends ventrad to the sternal area. There is a small group of setae cephalo-dorsad of the procoxacoila in most of the genera studied. This is the only group of setae located on the lateral aspect of the prothorax.

The prosternum of Chilocorus is the rectangular area located between the coxal fossae. There has been much controversy among morphologists as to the number of sclerites in this area. It is not my purpose to discuss this question, there are, however, a few landmarks of this region that must be considered. In all of the species studied there is a small pit, the furcina, (Fig. 3, *fur*) found near the meso-caudal boundary of each procoxacoria. There is a distinct ridge extending between these pits which probably serves as a place for the attachment of muscles. The prosternum of Chilocorus, Epilachna, Microweisea and Hyperaspis usually bears a few small setae and chalazae just cephalad of the procoxacoria, while in all of the genera of the Coccinellini it bears two distinct verrucae which are located adjacent to the meson.

Mesothorax and Metathorax

In general the mesothorax and metathorax of coccinellid larvae are so nearly similar that a single description will suffice for both of them. Each of these segments is wider than long, but in other respects they are similar to the prothorax in form.

The mesotergum in *C. bivulnerus* (Fig. 1, *mst*) is distinctly longer and narrower than the metatergum (Fig. 1, *mtt*). In practically all of the genera of the Coccinellini the mesotergum and metatergum are subequal in length, but the metatergum is as a rule wider than the mesotergum. In Microweisea, Scymnus, and Hyperaspis the mesotergum is longer and

narrower than the metatergum. The mesotergum and metatergum of *C. bivulnerus* do not bear dorsal shields. Each tergum bears a transverse row of four senti, the pinacula of which are distinct and never fused. The median senti are much smaller than the lateral ones. In Epilachna there is a small median dorsal shield from which two scoli project, these scoli originate so close together that they seem to be the two forks of a single scolus. In all of the genera of the Coccinellini the dorsal shield is present on the mesotergum and metatergum as a raised oval area which covers the larger part of the dorsum. The mesal margin of this shield bears a pair of small parascoli, while the lateral margin bears a large parascolus. The surface of the shield is densely covered with fine setae and in the genera Coccinella, Hippodamia, and Anatis also bears chalazae. In Scymnus and Microweisea the dorsal shield is weakly chitinized, covers the larger part of the dorsum, and bears a small verruca on each side of the meson. Hyperaspis, on the other hand, has no dorsal shield nor is there any chitinization to suggest the presence of a shield. The terga bear many long, black, prominent setae which are arranged in more or less transverse rows; one row on the cephalic and one on the caudal annulet of each segment.

The pleural areas of the mesothorax and metathorax of all of the species studied are well developed. They are the lateral vertical areas between the terga and the sterna (Fig. 2, *mspl*, *mtpl*). In *C. bivulnerus* the mesopleural area is much larger than the metapleural; this is also the case in Microweisea, Scymnus, and Hyperaspis. In Epilachna the metapleural area is larger than the mesopleural; while in all of the genera of the Coccinellini they are subequal. The ventral portions of the mesopleural and metapleural areas are obliquely crossed by a furrow extending caudomesad from the coxacoila. In *C. bivulnerus* the mesopleural area bears two subequal senti, one near the cephalic and one near the caudal margin; the base of each of these senti is provided with a small pinaculum. The metapleural area bears two senti, but the cephalic one is much smaller than the caudal. In Epilachna the cephalic area bears a few small setae, while the caudal one bears the large scolus. In the Coccinellini the cephalic area usually bears a few small setae, and the caudal one is provided with a parascolus in Hippodamia, Coccinella, and Anatis; while in Megilla and Adalia this area bears a struma. In Microweisea, Scymnus, and Hyperaspis the cephalic area is smaller than the caudal area which bears a small verruca in the two former, and a few fine setae in the latter.

The mesosternum and metasternum are so nearly similar to the prosternum that no description is necessary.

In *C. bivulnerus* the mesothoracic spiracle is located in the small triangular area lying between the mesotergum and the mesopleural area, the protopleurite (Böving 1917). This condition is also found in all of the

members of the Coccinellini and Epilachna; while in Microweisea, Scymnus, and Hyperaspis the mesothoracic spiracle is not located on the tergum, or protopleurite, as Böving points out, but distinctly in the mesocoria. The metathoracic spiracles are rudimentary or entirely wanting.

Appendages

The thorax of all coccinellid larvae bears three pairs of legs. One pair is attached to each segment. They are well developed and fitted for walking or clasping the surface of the leaves and stalks upon which the larvae are usually found. Since the general form and structure of each pair of legs is the same, their only difference being that of size, a description of a single prothoracic leg will suffice for all. The mesothoracic and metathoracic legs are subequal and slightly longer and wider than the prothoracic legs. Each leg is about as long as the body is wide, except in very young larvae in which they are distinctly longer. In adult larvae they are comparatively stout and fitted for clasping. The coxal fossae are the circular or oval holes in the sternum in which the legs are inserted. The coxa are attached to the coxal fossae by a distinct membrane, the coxacoria. There is a distinct coxacoila on the lateral margin of each coxal fossa in which the coxa articulates. The procoxa (Figs. 2 and 3, *prc*) is subcylindrical, short, tapering toward the distal end and bears a few scattered but prominent setae. The protrochanter (Figs. 2, 3, *prtr*) is short, triangular, the ventral surface the longer and bears a prominent group of coarse setae. The profemur (Fig. 3, *prfr*) is short, about twice as long as wide, with its dorsal, caudal, and cephalic surfaces sparsely setaceous. This condition of the femur is found in Chilocorus and Hyperaspis; while in Epilachna and all of the genera of the Coccinellini, and the genera Microweisea, and Scymnus, the femur is at least three times as long as wide. The protibia (Figs. 2, 3, *prti*) is about as long as the profemur, one-third as wide as long, and tapering distinctly toward the distal end. The cephalic, caudal, and dorsal surfaces of the proximal two-thirds are densely setaceous; while the entire surface of the distal one-third is densely covered with club-shaped setae or tenent hairs (Fig. 43, *te*). The tenent hairs are very numerous in Chilocorus, Epilachna, and all of the genera of the Coccinellini; while in Scymnus and Hyperaspis there are only a few, five to ten, on each tibia, and in Microweisea there are only two which are very broad, flat, elongated, and paddle-like (Figs. 44, 45). The protarsus (Figs. 2, 3, *prta*) consists of a single short triangular segment which bears a few tenent hairs. Its distal margin is provided with a sickle-shaped claw (Figs. 4, 3, *prcl*). This claw is provided with a short, blunt appendiculated tooth on its proximo-ventral angle, and it probably serves as an aid in clasping surfaces. There is some variation in the general shape of the tarsal claw in the various genera of the family and this characteristic serves as a means of separating them.

ABDOMEN

The abdomen of all coccinellid larvae is composed of ten segments which are connected by more or less distinct coria. This coria is usually more prominent on the ventral than on the dorsal aspect. The abdomen is generally subdepressed, widest on its cephalic half, and tapering on its caudal half. The abdomen in *C. bivulnerus* narrows gradually toward the caudal end. The first three segments are about as wide as the metathorax. This is also true of Epilachna and of all of the genera of Coccinellini in which the first, second, third, and fourth abdominal segments are subequal in width. The remaining abdominal segments become narrower toward the caudal end. In Microweisea and Scymnus the first, second, and third abdominal segments are the widest; caudad of the third the abdomen becomes narrower. In Hyperaspis the first, second, fifth, and sixth segments are subequal in width; while the third and fourth are the widest segments in the body.

In *C. bivulnerus* the first abdominal segment is slightly narrower and shorter than the metathorax. Its tergum (Figs. 1, 2) bears four distinct senti arranged in a transverse row. The dorsal senti are adjacent on the dorso-meson and the dorso-lateral ones are placed on each side near the lateral margin of the tergum. There is a small circular pinaculum at the base of each sentus. The dorsal pinacula are brown or yellow colored and the dorso-lateral ones are white. There is also a few inconspicuous setae on the surface of each pinaculum. The lateral aspect is a vertical area, almost square, and bears the large lateral sentus, at the base of which there is a very large pinaculum nearly covering the entire surface. The paralateral group is wanting. The sternum (Fig. 3, *st*) is about as long as the tergum. The coria between it and the metatergum is not at all distinct. The cuticle is thin and membraneous and bears two groups of small ventral setae adjacent to the ventro-meson. The ventro-lateral setae are wanting.

The external structure of segments two to five inclusive is similar, however, each succeeding segment is narrower than the preceding one. The coriae between the segments are distinct. Each tergum has four senti arranged in a transverse row. The dorsal senti and their pinacula are adjacent to the dorso-meson; the dorso-lateral senti are located in a position similar to those of the first abdominal segment. All of the pinacula are dark brown in color and bear numerous fine setae. Each lateral aspect is almost square and bears a distinct lateral sentus. The pinacula at the base of these senti are small. In the second and third segments ventrad of the lateral senti there is a solitary small seta; while in segments four and five there is a prominent chalaza surrounded by a group of small setae. This group represents the paralaterals. Each sternum is as long as its respective tergum and the coriae between the sterna are distinct. The cuticle is thin and membraneous and bears on each sternum four groups

of chalazae arranged in a transverse row; those near the meson are the ventral chalazae and those on the lateral margin are the ventro-laterals. Each chalaza is surrounded by a small group of setae.

The sixth, seventh, and eighth abdominal segments are as long as the preceeding but narrower. The pinacula at the bases of the dorsal senti have become fused on their mesal margins and appear to be dumb-bell-shaped. The dorso-lateral senti are shorter than those of the preceding segments and their pinacula are very much reduced. The lateral aspect of each of these segments is similar to that of the preceding, except that it is considerable smaller. There is a small lateral sentus with a very small pinaculum on the lateral aspect of the sixth and seventh segments and almost a rudimentary sentus on the eighth segment which is without a pinaculum. In Epilachna the lateral aspect of the seventh segment is provided with a distinct parascolus rather than with a scolus as in the sixth; while the eighth segment has a struma and the ninth only a few chalazae. There is a distinct chalaza surrounded by a group of fine setae ventrad of the lateral sentus of each segment. This chalaza and the setae represent a paralateral group. Each sternum is as wide and as long as its respective tergum. The cuticle of each segment is soft and bears four distinct chalazae arranged in a transverse row. Each chalaza is surrounded by a group of small setae. The ventral groups are adjacent to the ventro-meson and the ventro-lateral groups are located near the extreme lateral margin of each segment. The coriae between the segments are distinct.

The ninth abdominal segment is small, cylindrical, slightly narrower and shorter than the eighth. The tergum is inclined ventrad at an angle of about thirty degrees. The dorsal senti are absent and in their place there are distinct dorsal strumae. The dorso-lateral senti are also reduced to strumae and located near the lateral margin of the tergum. The lateral aspect is small and the senti are wanting, but there is a prominent chalaza surrounded by a group of setae near the ventral margin. This group represents the lateral group; the paralaterals are wanting. The ninth sternum is short, deeply emarginated on the caudal margin, and bears four chalazae arranged in a transverse row. The ventral chalazae are located adjacent to each other and the ventro-meson and are surrounded by a group of fine setae; while the ventro-lateral are without setae. Throughout the family the ninth segment shows the greatest variation in its size, shape, and structure. In Chilocorus the ninth abdominal segment is rectangular, about twice as wide as long; its anterior margin is little if any narrower than the eighth segment; the caudal margin is sharply rounded and never serrated; and its lateral aspect bears chalazae and setae. The lateral aspect of the ninth segment in Epilachna is rectangular, about twice as wide as long, much narrower than that of the eighth segment, and

with the caudal margin broadly rounded. Each lateral aspect bears a small chalaza. In all of the genera of the Coccinellini the ninth segment is more or less rectangular. The caudal margin is broadly rounded, usually widest near the middle, distinctly narrower than the eighth segment, and never crenulate or serrate. The lateral aspect is provided with numerous setae. In Microweisea the ninth segment is conical, about twice as long as wide, and much narrower than the eighth. The distal margins are sharply rounded and the tergum is chitinized and brown. The lateral aspect is provided with a few fine setae. In Scymnus the ninth segment is conical, about one-half as wide as long, much narrower than the eighth and not heavily chitinized. In Hyperaspis the ninth segment is semicircular, about twice as wide as long, and narrower than the eighth. The caudal margin is broadly rounded and never crenulate or serrate. The lateral aspect bears a few fine setae.

The tenth abdominal segment is as a rule not visible from the dorsal aspect. It appears to be a small ring of thin membrane surrounding the rosetted anal area. In the Coccinellini this membrane is often pigmented and appears black or brown colored. The rosetted appearance of the anal area is caused by the evagination of the rectum. This serves as a sucking disk and aids the larvae in locomotion.

In all the coccinellid larvae there are eight pairs of abdominal spiracles (Figs. 1 and 2, *abdsp*), a pair situated on each abdominal segment from one to eight inclusive. They are located near the cephalic margin of each tergum between the dorso-lateral and lateral senti in Chilocorus and Anatis, between the dorso-lateral and lateral scoli in Epilachna, between the dorso-lateral and lateral parascoli, strumae or verrucae in Hippodamia, Coccinella, Megilla, Adalia, and Scymnus, and between the dorso-lateral and lateral chalazae or setae in Hyperaspis.

There is a pair of repugnatorial pores on segments one to eight (Figs. 1, 2, *rp*). These pores are located on each lateral margin of the tergum in the coria between the segments. They emit a bad smelling fluid which is of a repulsive nature and serves to protect the larva from its enemies.

On each side of the dorso-meson in segments one to eight there are two small pits. There is another pair on each side of the tergum near the middle about midway between the dorsal and dorso-lateral senti of segments one to nine. All of these pits are arranged in a transverse row on the tergum. There is another pit on the lateral aspect of segments one to nine which is located immediately ventrad of the ventral senti. These pits are probably the points of attachment for muscles.

ARMATURE OF THE BODY-WALL

The armature of coccinellid larvae consists of spine-like setae on the body-wall or of conical, finger-like, or mound-like projections of the body-

wall which bear setae. They are known as scoli, senti, parascoli, strumae, verrucae, chalazae, or setae and vary greatly in form in the different tribes and genera of the family. After a study of the larvae of the Chrysomelidae, the probable progenitors of the Coccinellidae, one becomes convinced that Chelymorpha shows perhaps the greatest resemblance to the generalized coccinellids. In Chelymorpha each lateral margin of the body is provided with a longitudinal row of long branched projections of the body-wall. The distal end of each of these branches bears a stout seta. Fracker in his work on lepidopterous larvae called structures similar to these *scoli*. It was unfortunate, however, when he applied the same term to a non-branched projection of the body-wall which bears setae upon its trunk. These two structures are so widely different that they cannot be considered as one and the same thing and for the latter the name *sentus* is proposed. Fracker has also shown that the arrangement and number of setae on the prothorax represents the generalized condition in lepidopterous larvae. This may be true in coccinellid larvae, but there has been no attempt made in this work to homologize the setae or the projections that bear them. Since the arrangement of the setae in the various genera differs, especially on the abdominal segments, this character has been used to some extent in separating genera, and it is, therefore, necessary to adapt a tentative nomenclature for these structures. This nomenclature is based upon the conditions found in the third abdominal segment and has been applied only to the segments of the abdomen.

There is a seta or a projection bearing a seta or setae on each side of the dorso-meson. These are designated as the dorsal group. The projection on each lateral margin of the tergum is a dorso-lateral group, the one on the dorsal portion of the lateral aspect is a lateral group, the one on the ventral margin of the lateral aspect is the paralateral group, the small group on each lateral margin of the sternum is a ventro-lateral group, and the one on each side of the ventro-meson is the ventral group.

The scolus is a branched projection of the body-wall, usually more than five times as long as wide (Fig. 28). Each branch of the scolus bears at its distal end a single stout seta. The dorsal and lateral surfaces of the thorax and abdomen of Epilachna are provided with distinct scoli.

The parascolus is a modification of the scolus in which the projection is not more than three times as long as wide and usually not more than twice (Fig. 30). This structure bears a few short branches which are about as wide as long, each with a seta at its distal end. This modified scolus is designated as a parascolus. It is found in Hippodamia, Coccinella, and on the caudal segments of Anatis.

A sentus is an elongated, cone-like projection of the body-wall which is not branched like a scolus, but bears a few short stout setae upon its trunk (Fig. 29). Fracker called this a scolus, but it differs decidedly in

form from the true scolus and has been called a sentus. Senti are found in Chilocorous and Anatis. In the latter genus the senti are short and thick.

A pinaculum is the more or less chitinized plate which surrounds the base of a scolus, sentus, or parascolus (Figs. 28, 29, 30). It usually bears numerous, small, dark-colored setae. Several pinacula may become fused to form the shield-like plates of the body.

A chalaza is a distinct but slight pimple-like projection of the body-wall. It may be considerably wider than long and bears on its distal end a stout seta (Fig. 33). Chalazae are present in practically all coccinellid larvae. They are for the most part found on the sternum and in some cases on the lateral aspect. In Microweisea distinct chalazae are found on the dorsal aspect of the abdomen, there are also distinct chalazae on the dorsal shield in most of the genera of the family.

A struma is a parascolus which has become shortened, usually appearing to be nothing more than a distinct mound-like projection of the body-wall (Fig. 31) upon which are situated a few chalazae. This structure was formerly called a tubercule, but this term is misleading and has been applied by various workers to most any kind of an extension of the body-wall. In order to avoid further confusion the term struma is proposed for this structure. Strumae are found in the armature of the abdomen of Adalia and Megilla.

The struma becomes much reduced in some of the more specialized larvae so that it appears to be mound-like and bears setae instead of chalazae (Fig. 32). This structure has also been called a tubercule by some workers and by others a verruca. Since the term verruca is not misleading or conflicting, it should be restricted to structures such as these. Verrucae are found in the armature of Scymnus and very small indistinct ones in Microweisea; the latter genus also bears chalazae.

In the most specialized of the coccinellids verrucae and chalazae have become so greatly reduced that the setae are not elevated above the general surface of the body (Fig. 34). Setae are found on the body of all of the more generalized coccinellids, but it is only in the more specialized groups that the setae constitute the only type of armature. The Hyperaspini is the only tribe that I have studied which has this condition.

In the more generalized genera the armature of the body consists of scoli arranged upon the dorsal and lateral surfaces. Such a condition as this is found in the subfamily Epilachninae. In Chilocorous and Anatis the scoli are replaced by senti on the dorsal and lateral aspects and on these regions in Hippodamia, Coccinella, and to a small extent in Adalia parascoli are present. The projections of Adalia seem to show a stage of transformation between parascoli and strumae; for parascoli are found on the dorsal surface and strumae on the lateral. Strumae are found on the

dorsal and lateral regions of Megilla, but on the lateral aspect of the eighth segment there is a verruca. Verrucae are found almost exclusively on Scymnus, while in Microweisea they are very small and closely approximate the form of chalazae. Verrucae are also found on the ventral portion of the ninth segment in practically all genera of the Coccinellidae, the only exceptions being Hyperaspis and Scymnus. Chalazae are found on the dorsal shield and on the shield-like spots of the mesothorax and metathorax of Hippodamia, Megilla, Anatis, Adalia, and Coccinella. There are also a few on the prothoracic shield of Scymnus. The same type of armature is present on the ventral parts of the thoracic and abdominal segments throughout the family and on the lateral portions of the eighth and ninth segments of Adalia, Megilla, and Scymnus. They are usually surrounded by a group of finer setae. In Hyperaspis and its allies the armature of the body has been so reduced that it is composed of setae forming a hair-like covering over the entire surface. The ventral surface of all of the members of the family is provided with setae rather than scoli, parascoli, senti or strumae. Even in those genera where chalazae or verrucae are found on the ventral surface, setae are also abundant. The type of armature of the Coccinellidae shows a steady and unbroken series of changes in specialization from the generalized scolus to a seta through the reduction or the disappearance of parts.

SYNOPSIS OF LARVAE

In the taxonomic study of any group of organisms, the investigator should not draw conclusions from characteristics which upon the surface may show a high degree of specialization or generalization, without first making a careful study of these characteristics, no matter how important or unimportant they may seem. According to Comstock, "The logical way to go to work to determine the affinities of the members of a group of organisms is first to endeavor to ascertain the structure of the primitive members of this group; and then endeavor to ascertain in what ways these primitive forms have been modified by natural selection." With such a view as this in mind, the taxonomist must not only study the members of the group upon which he is working, but he must also endeavor to ascertain the conditions that existed in the progenitors of the group. It is obvious, then, that those conditions in the chosen group which are most nearly similar to the conditions in their progenitors are the most generalized; further, that those individuals possessing these primitive characteristics are the generalized individuals of the group. There are often two or more sets of prominent characters, and many times these may not run in parallel lines, but seem to contradict each other or to run in opposite directions. For instance in the larvae of the Coccinellidae that form which shows the most generalized condition of the head sutures, the Epilachninae, have also what seems to be the most highly specialized condition of the setae or scoli on the body; and Hyperaspini which have the most highly specialized condition of the head sutures show what appears to be the most generalized condition of the setae.

If one studies the conditions present in the Chrysomelidae, the probable progenitors of the Coccinellidae, he will find in the genus Chelymorpha conditions of the epicranial suture and scoli similar to those found in the Epilachnini. The epicranial stem in Chelymorpha is long and the epicranial arms are gradually divergent, a condition almost identical with that of the Epilachninae. The members of the subfamily Coccinellinae have a much shorter epicranial stem or in many genera it may be entirely wanting and the epicranial arms diverge immediately from the occipital foramen. Even the epicranial arms are wanting in the adult larvae of Scymnus and Hyperaspini; while the clypeal suture, which is distinct and entire in Chelymorpha and Epilachna, is incomplete and only indicated

on each margin of the head in the Coccinellinae. This fact tends to show a complete reduction of the sutures which are distinct in Epilachna and are entirely wanting or only slightly indicated in the Hyperaspini.

The condition of the armature of the body also shows a like reduction. In both Epilachna and Chelymorpha scoli are present. In Chilocorus the scoli are replaced by senti and in those forms which show a further reduction of the epicranial arms we find that there is a further reduction in the armature of the body. In Hippodamia, Coccinella, Adalia, Anatis, and Microweisea, forms in which the epicranial arms alone are present, the armature consists of parascoli, strumae, verrucae, and chalazae or setae; while in the Hyperaspini in which the epicranial suture is wanting the body is provided only with setae. The condition of the scoli in Epilachna might easily be taken as a highly specialized characteristic, but when one studies the characteristics of the progenitors of the Coccinellidae, he finds such a condition in the armature of the body as is found in the Epilachninae. There is a further likeness between the Chrysomelidae and the Epilachninae that seems also to be of importance, that is the food habits of the two are almost identical, as both are phytophagous. The Epilachninae are perhaps the only group of coccinellids that are entirely phytophagous in both the larval and adult stages.

The fact that the setae in Hyperaspini show an apparently generalized condition, while the epicranial suture is absent in the adult larval stages and present in the first larval stages, surely a specialized condition, does not interfere with this proposed classification. For specialization, as Comstock has pointed out, may take place in two wholly different ways. "First, by the addition or complication of parts, specialization by addition; second, by the reduction in the number or the complexity of the parts, specialization by reduction." The latter is considered to be the case in the Hyperaspini; the primitive scoli have been reduced to setae. Granting this to be true, we can readily see that these two wholly different characteristics, the condition of the scoli and the epicranial suture, show in a very striking way the presence of specialization in Hyperaspini and of generalization in the Epilachninae. In the first case there is the absence of the epicranial stem, only an indication of the clypeal suture, and a reduction of the scoli to setae; while in the latter there is the presence of the epicranial and clypeal sutures and of scoli similar in form to those of Chelymorpha.

Since, as Comstock has shown, there is such a thing as specialization by reduction and since the progenitors of the coccinellids, as nearly as we can ascertain, have an epicranial and a clypeal suture and a well-developed system of scoli, it seems to me altogether logical, and with the evidence at hand quite clear that the Epilachninae represent a generalized type of coccinellid larvae, though at a first glance they may appear to be highly specialized.

There is a great variation in the general structure of the larvae of the Coccinellidae. This variation ranges from the phytophagous type found in Epilachna to the extreme carnivorous type found in Scymnus and Hyperaspis. The larvae of the family possessing the phytophagous type of structure can very easily be mistaken for certain chrysomelid larvae which they resemble in general shape and in the arrangement of their scoli and pinacula, while those of the more carnivorous types might at first glance be mistaken for chrysopid larvae. The coccinellid larvae may be distinguished from this latter group by the development of the mandibles which are not so prominent in the coccinellids. The mandibles of all of the carnivorous coccinellids differ from those of the Chrysomelidae in that they are not so broad and have a smaller number of dentes; while in Epilachna they resemble very closely the chrysomelid mandibles. All of the coccinellid larvae examined possess three ocelli on the lateral portions of the head, while the chrysomelid larvae may possess from one to six or none on each side.

The Epilachninae are undoubtedly the most primitive type of coccinellid larvae, a fact which is shown by their likeness to their chrysomelid progenitors. Among the carnivorous coccinellids, Chilocorus is the most primitive, while Hyperaspis, which is the farthest removed from the chrysomelid larvae, shows the most specialized condition.

SUBFAMILIES OF COCCINELLIDAE

Epicranial suture present, epicranial stem extending one-half the distance from the occipital foramen to a line drawn through the antacoriae; clypeal suture present; antennae slender, more than three times as long as wide; body with scoli.....*Epilachninae*

Epicranial suture present or wanting, when present, the epicranial stem never extending one-half the distance from the occipital foramen to a line drawn through the antacoriae; clypeal suture never complete, only indicated on each side; antennae short, never more than twice as long as wide; body without scoli.....*Coccinellinae*

EPILACHNINAE

The body is elongate, oval to fusiform. The dorsal and lateral aspects are armed with scoli, the sternum with strumae or chalazae, and the head with a few long setae. The epicranial stem and epicranial arms are always present; the clypeal suture is entire and distinct. The antennae are more than three times as long as wide, inserted more than their own length dorso-mesad of the precoila. Each mandible is heavily chitinized, its mola not well developed, and the distal portion with several dentes of various lengths, the distal dentes the longest.

This subfamily is represented in North America by a single tribe, the Epilachnini. Casey says, "This tribe is represented in the United States

by two or three large pubescent species belonging to the single genus Epilachna." One species occurs in small numbers in southern Illinois. The Epilachninae are truly phytophagous. Our common species feeds almost entirely upon the squash plant and its relatives. The beetle is commonly called the squash lady-bug. This subfamily is represented in the material studied by a single species of the genus Epilachna Chevrolat.

Epilachna borealis Fab.—The prothorax is slightly chitinized with a transverse row of four scoli on the dorsum near its cephalic margin and a transverse row of small setae on its caudal margin; the pleural area is small and glabrous; the prosternum is short with two distinct setae on the ventro-meson; and the procoxacoriae are distant. The mesothorax and metathorax are subequal in length and width, the dorsum of each with four scoli, two on each side of the meson arising from the same pinaculum; the mesothoracic spiracles are located in the mesocoria; the metathoracic spiracles are wanting; the caudal portion of the mesothoracic and metathoracic pleural areas are each provided with a large prominent scolus; the mesothoracic and metathoracic sterna are each provided with a group of setae on each side of the ventro-meson; and the mesocoxacoriae and metacoxacoriae are distant. The coxa is short and subcylindrical; the trochanter is triangular, about as long as the coxa and bears a few setae; the femur is as wide as the trochanter, about twice as long and covered with numerous small stiff setae; the tibia is about as long as the femur and about two-thirds as wide, its dorsal and lateral surfaces are covered with short stiff setae, its ventral surface is thickly covered with fine setae, and the distal one-third is covered with tenent hairs; and the tarsus consists of a single segment which bears the heavily chitinized hooked claw and a few tenent hairs. The terga of the abdominal segments one to eight inclusive are similar. Each tergum is provided with four scoli, the dorsal scoli are adjacent to each other and the meson and the dorso-lateral scoli are on the lateral margins of the tergum. The ninth tergum bears four strumae which represent the dorsal and dorso-lateral groups; the tenth segment is membraneous. Each lateral aspect of segments one to six is provided with a prominent lateral scolus, of segments seven and eight with a lateral struma, and of segment nine with a lateral verruca. The paralateral group is represented by a prominent chalaza surrounded by a group of small setae ventrad of each lateral scolus. Sternum one is provided with two prominent ventral chalazae, the ventro-laterals are wanting; sterna two to nine bear two adjacent ventral chalazae and two ventro-lateral chalazae located near the lateral portion of each sternum; and sternum ten is crescent-shaped and armed with setae. The rectum is evaginated to form a disk-like sucker. It is used as an aid in locomotion.

COCCINELLINAE

The body is elongate to oval, dorsal surface convex, ventral surface concave or flat. The body-wall is provided with senti, strumae, verrucae, chalazae, or evenly distributed setae. The head is provided with long distinct setae. The epicranial stem and epicranial arms may be present or wanting, when present, the epicranial stem never extends more than one-third of the distance from the occipital foramen to a line drawn through the antacoriae. The clypeal suture is never entire, but is usually indicated by a distinct furrow which extends mesad on each side from the precoila. The antennae are never more than three times as long as wide, consist of three segments, and are inserted about midway between the ocelli and the precoilae. The mandibles usually have one, two, or three teeth at the distal end, and the proximo-mesal margin is provided with a triangular or mound-shaped mola.

This subfamily includes all of those tribes the members of which are carnivorous. They may also be phytophagous to the extent that they may eat fungi and probably small amounts of pollen.

Tribes of Coccinellinae

1(6) Epicranial arms always present; epicranial stem always present in all larval stages unless obliterated by the separation of the epicranial arms.....2

2(3) The dorsum of the body armed with senti six to eight times as long as wide; the epicranial stem extending one-third of the distance from the occipital foramen to a line drawn through the antacoriae; epicranial arms gradually divergent.....*Chilocorini*

3(2) The dorsum of the body never armed with senti six to eight times as long as wide.....4

4(5) Dorsum of the body armed with short senti, parascoli, or strumae; epicranial stem, when present, never extending one-third the distance from the occipital foramen to a line drawn through the antacoriae; epicranial arms gradually or abruptly divergent .....*Coccinellini*

5(4) Dorsum of the body provided with small verrucae or setae; epicranial stem always obliterated by the separation of the epicranial arms, epicranial arms diverge from the occipital foramen .....*Microweiseini*

6(1) Epicranial stem and epicranial arms never present in adult larvae 7

7(8) The dorsal and lateral aspects of the body with strumae or verrucae.....*Scymnini*

8(7) The dorsal and lateral aspects of the body with fine slender setae .....*Hyperaspini*

Chilocorini

The body is subovate, widest at the metathorax. The first three abdominal segments are slightly narrower than the metathorax, segments four to eight are successively narrower, segment nine is about as wide as long, its caudal margin is broadly rounded and its lateral margin is provided with a distinct struma; and segment ten is small and directed ventrad. The dorsal and lateral aspects of the body are provided with long senti the length of which varies on the different portions. The epicranial stem and epicranial arms are present. The epicranial stem extends about one-third of the distance from the occipital foramen to a line drawn through the antacoriae, divides and forms the two epicranial arms which diverge gradually for a short distance, then widely, and finally each extends laterad to a point dorsad of an antacoria and ventrad of an ocellus where it becomes obsolete. The mandibles are triangular in outline, heavily chitinized, the apex is bifurcated, and the proximo-mesal margin is provided with a distinct mola.

This tribe is represented in the material studied by the single genus Chilocorus Leach.

Chilocorus bivulnerus Muls.—The head is chitinized, dark, and provided with numerous setae. The epicranial stem and epicranial arms are distinct; the clypeal suture is indicated on each lateral margin of the head. The mouth is directed cephalo-ventrad. The prothorax is provided with a large dark colored dorsal shield bearing ten senti, six of which are arranged in a transverse row near the cephalic margin. The lateral aspect of the prothorax bears a small group of setae cephalo-dorsad of the procoxacoria. The cephalic portion of the prosternum also bears a small group of setae on each side of the meson. The procoxacoriae are distant. The mesotergum is distinctly longer and narrower than the metatergum. Each is provided with four large senti arranged in a transverse row; the dorsal senti are distinctly smaller than the lateral ones. The pinacula are small and bear distinct setae. The mesopleural area is longer than the metapleural; both areas are obliquely crossed by a distinct furrow. The cephalic portions of the mesopleural and metapleural areas are subequal in size, triangular, and each provided with a large sentus. The mesothoracic spiracle is located in the mesocoria near the cephalic margin of the mesothoracic sentus; the metathoracic spiracle is rudimentary or wanting. The caudal portions of the mesopleural and metapleural areas are unequal in size, that of the metapleural area is much larger than that of the mesopleural. The cephalic metapleural sentus is about one-half as long as the caudal one. The mesosternum and metasternum are similar in size and shape. The mesocoria is distinct while the metacoria is obscure. The cephalic portions of the mesosternum and metasternum are each provided with a chalaza on each side of the ventro-meson; these chalazae are sur-

rounded by groups of setae. The legs are about as long as the body is wide and the tibia is very densely setaceous.

The first abdominal segment is shorter than the metathorax and its tergum bears four senti arranged in a transverse row; the dorsal pinacula are yellow and the dorso-lateral ones are white; the lateral aspect is rectangular with a large lateral sentus the pinaculum of which covers the greater part of the lateral surface and the paralaterals are wanting. The sternum is about as long as the tergum, the ventral setae are adjacent on the ventro-meson while the ventro-laterals are wanting. Abdominal segments two to five are similar, narrower than the first; their terga are subequal in length, the dorsal and dorso-lateral senti of each segment are arranged in a transverse row, and each sentus is provided with a distinct pinaculum. The lateral aspect is nearly square; the lateral senti are larger than the dorso-lateral, their pinacula are small. Ventrad of the second and third lateral senti, there is a small paralateral seta and ventrad of the fourth and fifth lateral senti, there is a paraleteral group of setae surrounding a distinct paralateral chalaza on each segment. The sterna are as long as their respective terga, slightly chitinized, their coriae are distinct, and each bears four chalazae arranged in a transverse row, each chalaza surrounded by six or eight small setae. Segments six, seven, and eight are each narrower than the preceding ones. Their dorsal pinacula are fused and the dorso-lateral senti are shorter than the dorso-lateral senti of segments two to five. Their lateral aspects are smaller, but are similar in shape to those of the preceding segments, the lateral aspects of the sixth and seventh segments are provided with small lateral senti, while the lateral sentus of the eighth segment is much reduced and the pinaculum is absent. Ventrad of each lateral sentus, there is a paralateral chalaza surrounded by a group of setae. The sterna are as wide as the terga, their coriae are distinct, and the ventral and ventro-lateral groups of setae surrounding the chalazae are present. The ninth abdominal segment is about as wide and about as long as the eighth, cylindrical, and inclined ventrad. Its tergum is shield-shaped and has two distinct dorsal verrucae near the caudo-mesal margin, the dorso-lateral verrucae are wanting. Its lateral aspect is small, each with a distinct lateral verruca, ventrad of the verruca there is a distinct paralateral chalaza surrounded by a group of setae. Its sternum is short, deeply emarginated on the caudal margin, the ventral and ventro-lateral groups of chalazae are present, and the ventral chalazae are surrounded by a few setae while the ventro-laterals are represented by a single chalaza. The tenth segment is small, not visible from the dorsal aspect and the rectum is evaginated to form a disk-like sucker. There is a pair of repugnatorial pores located in the coriae of segments one to seven about one-half the distance between the dorsal and dorso-lateral senti.

Coccinellini

The body is fusiform or elongate, widest at the metathorax, usually highly colored with black, red, yellow, orange, or blue; never with senti except in Anatis in which the senti are short and thick, but never five times as long as wide, usually with parascoli or strumae. The abdomen becomes gradually narrower toward the caudal end. The ninth abdominal segment is about twice as long as wide, never wider than long as in Chilocorini or Hyperaspini, never with lateral parascoli or strumae as in Chilocorini, dorsum provided with a light colored, slightly chitinized shield bearing many setae or chalazae. The head is heavily chitinized, the epicranial stem, if present, never extends one-third the distance from the occipital foramen to a line drawn through the antacoriae; the epicranial arms are usually widely divergent. The mouth is directed cephalo-ventrad.

The members of this tribe are more numerous in Illinois than those of any of the other tribes. They are almost wholly carnivorous, their only plant food being either fungi or in some cases pollen grains.

Genera of Coccinellini

1(2) Epicranial stem and epicranial arms always present; terga one to eight with strumae usually bearing three distinct chalazae and densely covered with fine setae..... *Megilla*
2(1) Epicranial arms always present; epicranial stem obliterated by the separation of the epicranial arms.....3
3(4) Terga one to eight with senti, not five times as long as wide. *Anatis*
4(3) Terga one to eight without senti.....5
5(8) Terga one to eight with parascoli or strumae which bear more than five chalazae and are sparsely setaceous.....6
6(7) Tarsal claw with a distinct appendiculated tooth at its proximal end..... *Coccinella*
7(6) Tarsal claw without a distinct appendiculated tooth at its proximal end..... *Hippodamia*
8(5) Terga one to eight with strumae which never bear more than five prominent chalazae and the surface of the strumae densely setaceous..... *Adalia*

Megilla Mulsant

This genus is represented in the material studied by a single species.

Megilla maculata DeGeer.—The body is elongate, widest at the mesothorax and metathorax. Its general color is black and mottled with light yellow or cream-colored areas. The head is heavily chitinized, the dorsal portion dark and the ventral portion more or less white. The epicranial stem is present as a short line or suture on the dorsal portion of the head. It extends about one-fifth of the distance from the occipital foramen to a

line drawn through the antacoriae. The epicranial arms diverge laterad and ventrad and become obsolete slightly mesad of the antacoria. The mouth is directed ventrad. The cephalic margin of the prothoracic shield is provided with two small cream-colored spots, and the caudal margin with a yellow boundary. The mesothorax and metathorax have a shield-shaped cream-colored area on the dorso-meson; the cephalic portion of the mesothoracic and metathoracic lateral aspects are also cream-colored. There is a light colored area on the dorso-lateral portions of abdominal segments one to eight. On the lateral portion of the first segment, and on the tergum and lateral aspects of the fourth and fifth segments, the cuticle is yellow. The ventral aspect of the entire larvae is tan colored. The prothoracic shield is provided with many chalazae and numerous setae, the terga of the mesothorax and metathorax are provided with a large struma-like shield which bears six to eight chalazae. The lateral aspect of the prothorax is glabrous. The mesothoracic spiracles are situated in the mesocoria near the cephalic margin of the lateral aspect and each spiracle is surrounded by three or four small, black setae. The cephalic portion of the lateral aspect of the metathorax has three or four setae, but the metathoracic spiracles are wanting. The caudal portions of the mesothorax and metathorax are about twice as large as the cephalic and provided with a struma-like plate which bears six to eight chalazae. The sternum of all of the thoracic segments is provided with a small pair of verrucae adjacent the meson near the cephalic margin of the segment. Each tergum of segments one to eight is provided with a transverse row of four strumae, two dorsal and two dorso-laterals. Each struma usually bears three distinct chalazae. The lateral aspect of segments one to eight is each provided with a large lateral struma with four to eight chalazae, of segments two to eight with a small mound-like paralateral struma usually with one large chalaza and many seta on each segment. Each sternum of segments one to eight has a transverse row of four chalazae, each chalaza surrounded by a few setae. The ventro-lateral group is wanting on the first sternum. The tergum of the ninth segment is longer than wide, shield-shaped, its cephalic margin slightly emarginated, darkly colored and densely setaceous. The lateral aspect is much reduced and bears a single large lateral chalaza, the paralaterals are wanting. The sternum is shorter than the tergum, the caudal margin deeply emarginate with the ventral and ventro-lateral chalazae distinct. The tenth segment is not visible from the dorsal aspect, slightly setaceous, and appears to be cylindrical when viewed from the ventral aspect. The legs are long and slender, about one and one-half times as long as their thoracic segment is wide.

Anatis Mulsant

This genus is represented in my material by a single species.

Anatis 15-punctata Oliv.—The body is elongate, widest at the meta-

thorax. The dorsal portion of the head is dark colored while the ventral part of the face is white or yellow. The epicranial stem is absent, the epicranial arms extend cephalad and ventrad from the occipital foramen for a short distance and diverge widely laterad and ventrad; they become obsolete dorso-mesad of the antacoriae. The mouth is directed cephalo-ventrad. The mesothorax, metathorax, and the first eight abdominal segments bear short stout senti from one to five times as long as wide. The prothorax has a distinct parascoli on the caudo-lateral margin of the dorsal shield. There are four or five chalazae cephalad of this parascoli. The caudo-mesal portion of the dorsal shield is provided with a distinct yellow or white shield-shaped area, the cephalic portion of which bears two chalazae adjacent to the meson. The mesal and lateral tergal senti of the mesothorax and metathorax arise from the dorsal shields of their respective segments. The caudal portions of the lateral aspects of the mesothorax and metathorax are each provided with a small sentus. The mesothoracic spiracles are located in the mesocoria and the metathoracic spiracles are rudimentary or wanting. The thoracic sterna are all similar, the sternum of each segment has a pair of small verrucae adjacent to each other and the ventro-meson, the coxacoriae are distant. The first to eighth segments of the abdomen are subequal in length. Their terga are provided with four senti arranged in a transverse row; the dorsal senti of the sixth, seventh, and eighth segments have their pinacula fused on each segment, and the dorso-lateral senti of the seventh and eighth segments are short and inconspicuous. The metathorax and the first abdominal segment are each provided with a small cream-colored area caudad of and about one-half the distance between the dorsal and dorso-lateral senti. The lateral aspects of the first and second abdominal segments are white, each with a distinct white lateral sentus and pinaculum; the lateral aspects of the third to eighth segments are cream-colored with their senti and pinacula brown; the lateral aspects of the seventh and eighth segments are without lateral senti but are provided with lateral verrucae while ventrad of each lateral sentus or verruca, except in the first, ninth, and tenth segments, there is a distinct chalaza surrounded by a few setae which represent the paralateral group. The sterna of the first to the eighth segments are similar in shape, except that they become narrower toward the caudal extremity. The first sternum has two ventral chalazae adjacent to the meson, the ventro-laterals are wanting, while in sterna two to eight the ventral and ventro-lateral groups are present on each segment. In the eighth and ninth segments the ventral and ventro-lateral groups on each side have become fused so that there appears to be a single pair on each side of the meson. The tergum of the ninth segment is longer than wide, shield-shaped, and with many setae on its surface; its lateral aspect is much reduced and bears small and indistinct lateral verruca, the paralaterals

are wanting; and its sternum is provided with ventral and ventro-lateral chalazae. The tenth tergum is not visible from the dorsal aspect and the greater part of its ventral aspect is hidden by the evaginated rectal disk. The legs are long and slender, about one and one-half times as long as the metathorax is wide.

Coccinella Linné

The body is fusiform, elongate and widest at the metathorax. The head is usually light-brown colored and provided with many setae. The epicranial arms diverge immediately from the occipital foramen and become obsolete near the antacoriae. The mouth is directed ventrad and slightly cephalad. The thoracic segments are provided with a dorsal shield. The dorsal and dorso-lateral aspects of abdominal segments one to eight are provided with parascoli or verrucae, the ventro-lateral aspect with verrucae, and the ventral aspect with verrucae or chalazae surrounded by a few setae. The dorsum of the ninth abdominal segment is shield-shaped and densely setaceous, the ventral aspect is provided with verrucae or chalazae, and is about one-half as long as the dorsal aspect. The legs are well developed, stout, and extend beyond the lateral margins of the body. The coxacoriae are distant. The basal portion of the tarsal claw is provided with a distinct appendiculate tooth.

Species of Coccinella

Terga one to eight with distinct parascoli; prothoracic shield with two distinct, longitudinal, dark, heavily chitinized areas on each side of the meson.....*C. 9-notata*

Terga one to eight with strumae; prothoracic shield with a single, dark, heavily chitinized area on each side of the meson.....*C. sanguinea*

Coccinella 9-notata Herbst.—The body is fusiform, usually stout, and widest at the metathorax. The dorsal and dorso-lateral surfaces are provided with parascoli, and the ventro-lateral surface with small verrucae. The general color is light grayish-brown to dark tan or brown marked with white or lemon-yellow areas. The dorsal portion of the head is light-brown and the face is cream-colored. The epicranial arms diverge from the occipital foramen and the mouth is directed slightly ventrad and cephalad. The prothorax is wider than long and oval in outline; the dorsal shield covers the greater part of its dorsal surface and bears four distinct, dark-colored, longitudinal areas; and the cephalic, lateral, and part of the caudal margins are provided with chalazae. The mesothorax and metathorax are subequal in size, each is about twice as wide as long and each dorsal surface is provided with a small oval dorsal shield on each side of the meson. There is a small dorso-lateral parascolus on the caudo-lateral portion of both the mesothorax and metathorax. Each thoracic sterna is provided with a pair of verrucae which are adjacent to the ventro-meson.

The dorsal and dorso-lateral portions of abdominal segments one to eight are provided with parascoli. The dorsal parascoli are brown, while the dorso-lateral and lateral ones of the first and fourth segment are white or cream-colored, and also the area near the pinacula of these parascoli is white. Segments two to nine are provided with paralateral verrucae, while segment one has a small paralateral chalaza. The sterna of segments two to nine are provided with four verrucae arranged in a transverse row on each sternum; while the sternum of the first segment has only two verrucae, the ventro-lateral ones are absent. The ventral and ventro-lateral verrucae on either side of the meson of the ninth segment are almost fused so that there seems to be only two on this segment. The dorsal surface of the ninth segment is about twice as long as the ventral, shield-shaped, the caudal margin is rounded, and densely setaceous. The legs are well developed, long, and stout. The proximal portion of the tarsal claw is provided with a distinct appendiculate tooth.

Coccinella sanguinea Linn.—The body is elongate and widest at the metathorax. The dorsal and lateral surfaces are provided with strumae, and the ventral surface with verrucae or chalazae. The general color of the body is light to dark brown, mottled or spotted with yellow or cream-colored areas. The head is light brown and the face is yellow. The mouth is directed ventrad and slightly cephalad. The prothorax is about three-fourths as long as wide, and the caudal margin is slightly emarginated. The dorsal shield is light brown in color, entire, with a light yellow line on the meson, and the cephalic and lateral margins are provided with chalazae. The mesothorax and metathorax are subequal in size, about twice as wide as long, each with a small oval shield on either side of the meson. There is a light yellow area on the meson between the shields of each segment. The mesothoracic spiracles are located in the mesocoria cephalo-dorsad of the mesocoxacoilae, the metathoracic spiracles are rudimentary. The caudal portion of the lateral aspect of the mesothorax and metathorax bears a small verruca. The sterna of all of the thoracic segments are provided with a pair of small verrucae adjacent to each other and the meson. Abdominal segments one to eight are provided with dorsal and dorso-lateral strumae, and each segment bears more than five chalazae and a few scattered setae. The dorsal strumae of the fourth abdominal segment, the dorso-lateral strumae of the first and fourth segments, and the lateral strumae of the first, fourth, and fifth segments are white or light yellow. There is a small paralateral struma, which in many cases appears to be verruca-like, located ventrad of each lateral struma, except in the first abdominal segment where it is wanting. The sterna of segments one to nine are each provided with ventral and ventro-lateral groups of chalazae, except in the first segment, where the ventro-lateral groups are wanting. The dorsum of the ninth segment is shield-shaped with the

caudal margin rounded, is twice as long as its sternum, is dark colored, and bears many short setae. The legs are long, slender, well developed, and the tarsal claw is provided with a distinct appendiculate tooth at its proximal end.

Hippodamia Mulsant

The body is fusiform, elongate, and usually widest at the metathorax. The head is brown to dark colored and distinctly setaceous. The epicranial arms diverge immediately from the occipital foramen and become obsolete near the antacoriae. The mouth is directed ventrad and slightly cephalad. The dorsum of each thoracic segment is provided with distinctly chitinized shield-shaped areas which constitute the dorsal shields. The dorsal and dorso-lateral aspects of the body are provided with parascoli. The tergum of the ninth abdominal segment is shield-shaped, setaceous, and with the caudal margin broadly rounded. The ventro-lateral aspect of the body is provided with small strumae; while the sterna are all provided with verrucae. The legs are well developed, extend beyond the sides of the body, stout, and with the tarsal claw not provided with a distinct appendiculate tooth at its proximal end. The coxacoriae are distant.

Species of Hippodamia

Dorsal shield with two brown or black chitinized plates on each side of the meson.....*H. convergens*
Dorsal shield with a single brown or dark chitinized plate on each side of the meson.....*H. 13-punctata*

Hippodamia convergens Guer.—The body is elongate, widest at the metathorax, and the dorsal and lateral surfaces are provided with parascoli. The general color of the body is dark-brown to black, marked with yellow, orange, red, or white. The head is dark-brown to black, the face is lighter than the dorsal part. The epicranial arms diverge immediately from the occipital foramen and become obsolete dorso-mesad of the antacoriae. The mouth is directed ventrad and slightly cephalad. The prothorax, when viewed from above, is oval in outline and wider than long. The dorsal shield is provided with four longitudinal dark colored areas separated by white or orange colored bands. The cephalic and lateral margins of the dorsal shields are provided with chalazae. The dark plate-like spots also bear chalazae and resemble strumae. The mesothorax and metathorax are subequal in length. The dorsal surface of each is provided with parascoli, the pinacula of which have grown together on each side of the meson to form a basal shield. The cephalic portion of each lateral aspect of the mesothorax bears a mesothoracic spiracle, the metathoracic spiracle of each side is rudimentary. The caudo-lateral aspect of the mesothorax and metathorax are each provided with a distinct parascolus, the

mesothoracic one is brown and the metathoracic one is white or cream-colored. Each thoracic sternum is provided with a pair of verrucae adjacent to the meson. The terga of abdominal segments one to eight are provided with black or brown parascoli, except the fourth, in which the parascoli are orange colored. The dorso-lateral parascoli of segments one and four are also yellow or orange colored. The lateral aspect is provided with a row of lateral parascoli, those on the first and fourth segments are white and the remainder are brown. The lateral aspect is also provided with a row of brown paralateral strumae ventrad of the lateral parascoli. Sterna two to nine are provided with a transverse row of four verrucae on each segment, sternum one bears only two ventral verrucae which are adjacent on the ventro-meson, the ventro-lateral verrucae are absent. The dorsum of the ninth abdominal segment is shield-shaped, twice as long as its sternum, and provided with many setae or chalazae. The legs are well developed and extend beyond the sides of the body. The tarsal claw is without an appendiculate tooth.

Hippodamia 13-punctata Linn.—The body is slender, elongate, widest at the metathorax. The dorsal and lateral surfaces are provided with parascoli. The general color is brownish-tan to dark grayish-brown and the head is darker than the remainder of the body. The head is heavily chitinized, the epicranial arms do not meet but extend separately to the occipital foramen. The mouth is directed cephalo-ventrad. The prothorax is wider than long, and when viewed from above, is oval in outline. Its entire surface is covered with a solid brown dorsal shield which has a fine white line running along the dorso-meson. The cephalic, lateral, and caudal margins are provided with distinct chalazae. The mesothorax is slightly longer than the metathorax, about twice as wide as long, with a distinctly chitinized, oval, shield-shaped struma on either side of the meson. This struma bears ten to fifteen chalazae. The metathorax is more than twice as wide as long and provided with a chitinized shield-like struma on each side of the meson. This struma bears about as many chalazae as the mesothoracic strumae. The cephalic portion of the lateral aspect of the mesothorax and metathorax bears the thoracic spiracles. The mesothoracic spiracles are prominent and are located in the mesocoria cephalo-dorsad of the coxacoriae, the metathoracic spiracles are rudimentary. The caudal portion of the lateral aspect of the mesothorax is provided with a brown struma, while the metathorax is provided with a white struma. Each thoracic sterna is provided with two distinct verrucae adjacent to the ventro-meson. The legs are well developed and extend beyond the sides of the body. The tarsal claw is without a distinct appendiculate tooth. The terga of abdominal segments one to eight are provided with distinct dorsal parascoli located near the dorso-meson, those on the fourth abdominal segment are white. The lateral margins of terga

one to eight bear the dorso-lateral parascoli, the first and fourth are white and the remainder are brown to dark tan-colored. The ninth abdominal segment is longer than wide; its caudal margin is acutely rounded; its dorsal surface is brown colored, chitinized, and bears many chalazae and small setae. The lateral aspect of segments one to eight is provided with distinct lateral strumae, those on segments one and four are white. There is a small paralateral verruca ventrad of each lateral strumae. The lateral aspect of the ninth segment bears chalazae. The sterna of segments two to nine are provided with four chalazae arranged in a transverse row on each segment, the sternum of the first segment has only two chalazae present, the ventro-laterals are wanting.

Adalia Mulsant

This genus is represented in the material studied by a single species.

Adalia bipunctata Linn.—The body is elongate, oval in outline, the third and fourth abdominal segments are the widest. The general color is dark brown to bluish-gray, mottled with light yellow or cream-colored spots. The dorsal part of the head is dark brown to black and heavily chitinized, while the ventral portion of the front and clypeus is white or cream-colored. The epicranial stem is absent and the epicranial arms curve broadly laterad and mesad to the pretentorinae, giving the front a more or less circular appearance, then extend laterad from the pretentorinae toward the antacoriae near which they become obsolete. The mouth is directed cephalo-ventrad. The prothorax is crossed longitudinally by a median and two lateral yellow stripes. The dorsal shield is not united to the meson of the mesothorax and metathorax and the two portions are separated by a cream-colored area. The lateral aspect of the prothorax is glabrous. The cephalic portion of the mesothorax and metathorax is also glabrous; while the caudal portion is large and bears a small but distinct struma on each segment. The mesothoracic and metathoracic spiracles are located in the coriae between the segments. The thoracic sterna are distinct, each sternum bears a pair of small verrucae near its cephalic margin. The coxacoriae are distant. Abdominal segments one to eight are each provided with a transverse row of four strumae on the tergum. The mesal portions of the dorsal strumae of the fourth segment are white, while the lateral portions are brown, the dorso-lateral strumae of the first segment are surrounded by a distinct white area, and the dorso-lateral strumae of the second to the eighth segments are surrounded by a much smaller white area. Each struma is provided with three to five prominent chalazae. The lateral aspect of segments one to eight is yellow and the strumae are brown except on the fourth segment where they are light yellow. There is a small but distinct chalaza on each segment ventrad of the lateral strumae of segments one to eight which is surrounded by a few

setae representing the paralateral group. The ninth tergum is shield-shaped, longer than wide, the caudal margin concave and provided with numerous setae, while the cephalic margin bears only a few chalazae. The tenth tergum is visible from the dorsal aspect as a small, brown colored, chitinized area caudad of the ninth tergum and is provided with a single chalaza on each side of the meson. Each of these chalaza is surrounded by a group of small setae. The ninth sternum is about one-half as long as its tergum, deeply emarginate on its caudal margin, and bears two chalazae on each side of the meson, each of which is surrounded by a few setae. The tenth sternum is longer than its tergum and bears a dark colored spot near the lateral margin. The legs are slender, well developed, and longer than the body is wide.

Microweiseini

The body is small, elongate, fusiform, depressed, widest at the metathorax, provided with setae, and light-brown to yellowish-tan colored. The head is dark-brown to black in color and chitinized. The mouth is directed cephalo-ventrad and the mandibles are unidentate. The epicranial arms diverge slowly from the occipital foramen and become obsolete near the antacoriae. The spear-shaped front and post-clypeus are divided on the meson by a distinct, dark colored, chitinized bar which extends from the occipital foramen to the clypeo-labral suture. The prothorax is oval and slightly wider than long; while the mesothorax and metathorax are distinctly wider than long. The terga of the thoracic segments are longitudinally crossed by a small dark-colored area on each side of the meson, more distinct on the prothorax than on the mesothorax or metathorax. The ninth abdominal segment is conical, narrower than the eighth, and about twice as long as wide. The legs are well developed and extend beyond the sides of the body; the tibiae are provided with two paddle-shaped tenent hairs at the distal end; the tarsal claw bears a distinct appendiculate tooth; and the coxacoriae are distant.

MICROWEISEA Cockerell

This genus is represented in the material studied by a single species.

Microweisea misella Le Conte.—The body is fusiform, elongate and light-brown to yellowish-tan in color. The head is elongate, dark colored, and chitinized. The epicranial arms are present, but the epicranial stem is wanting. There is a dark-brown heavily chitinized bar extending along the dorso-meson from the occipital foramen to near the clypeo-labral suture. The mouth is directed cephalad. The prothorax is wider than long and somewhat oval in outline. There are two brown chitinized spots near the middle of the dorsum adjacent to the meson. The dorsum is provided with a very few short setae. The mesothorax and metathorax

are about twice as wide as long; and the lateral margin of each is provided with a fringe of fine setae. The sterna of the thoracic segments are equal in size to that of their respective terga. The prosternum appears to be glabrous; while there is a pair of small verrucae adjacent to the ventromeson of the metathorax and mesothorax. These verrucae are provided with setae which are about as long as their segments. The coxacoriae are distant and placed near the lateral margins of the sterna. The legs are small, well developed, and extend beyond the sides of the body. Each tibia is provided with two paddle-like tenent hairs placed near the distal end of the segment, the tarsal claw bears a distinct appendiculate tooth. Abdominal segments one to eight are similar, except that they become successively smaller. Each tergum is provided with a few small setae which are never as long as the segments. The dorsum of the eighth segment is dark, chitinized, and its caudal margin is not emarginate. The sterna and the lateral aspects of segments one to eight are similar in general size and structure. They are membraneous and provided with a few small setae. The coriae between the segments are distinct. The sternum of the eighth segment is deeply emarginate on its caudal margin. The ninth segment is longer than wide, its caudal margin narrower than the cephalic. The tergum is shield-shaped, dark-colored, chitinized, and the caudal margin is acutely rounded and bears many setae about one-half as long as the segment is wide. The shape of the ninth sternum is similar to that of its tergum, it is very slightly chitinized and supplied with only a few setae. The tenth segment is cylindrical, directed caudo-ventrad; the rectum is evaginated to form a sucking disk.

Scymnini

The body is small, elongate, fusiform, widest caudad of the metathorax, provided with verrucae or chalazae and setae, and light-yellow to light-brown in color. The head is slightly chitinized, light colored, densely setaceous, and directed cephalad. The epicranial suture is wanting. The prothorax is oval, slightly chitinized, and provided with verrucae. The mesothorax and metathorax are about twice as wide as long and are provided with verrucae on the dorsal surfaces and with chalazae and setae on the lateral and ventral surfaces. The abdominal segments are provided with verrucae on the dorsal and lateral surfaces and with chalazae and setae on the ventral. The ninth abdominal segment is cylindrical, about twice as long as wide and the sternum is shorter than the tergum. The legs are well developed and extend beyond the sides of the body, the tibiae bear more than two tenent hairs, and the coxacoriae are distant.

Scymnus Kugelann

This genus is represented in my material by a single species which could not be determined.

Scymnus sp.?—The body is fusiform, elongate, flattened, light-yellow or cream-colored to light-brown. The head is circular in outline, very slightly chitinized, and provided with numerous black setae which are about one-half as long as the body is wide. The epicranial suture is entirely wanting and the mouth is directed cephalad. The prothorax is slightly wider than long, and the dorsum bears the light-brown slightly chitinized dorsal shield. The cephalic margin is provided with six large black setae which are about one-third as long as the segment, the caudal margin has six setae of about the same size as the cephalic setae, but not so darkly colored; midway between the cephalic and caudal rows there is another of four long black setae. The mesothorax is distinctly narrower and shorter than the metathorax which is broadly emarginate on its caudal margin. Both the mesothorax and metathorax have an oval-shaped verruca on either side of the dorso-meson. This verruca is provided with setae which are about as long as the verruca is wide. The thoracic sterna are distinct. Those of the mesothorax and metathorax are provided with a few setae; while the prothoracic sternum is glabrous. The coxacoriae are distant and the legs are well developed, usually white or light-yellow in color, and extend beyond the margins of the body. Each tibia is provided near the distal end with six to eight tenent hairs. The tergum of the first abdominal segment is distinctly longer than the second. Each tergum of abdominal segments one to eight is provided with a transverse row of four distinct verrucae. The dorsal verrucae are adjacent to the dorso-meson and the dorso-lateral are near the lateral margin of the tergum in each segment. The lateral aspect of segments one to seven is lobed and each lobe bears a distinct verruca with setae as long as the segment bearing them. The lateral aspect of the eighth segment bears two or three chalazae about as long as the setae on the verrucae. There are on segments two to eight one or two distinct paralateral chalazae immediately ventrad of the lateral verrucae and chalazae, while the first segment bears a small paralateral seta. The sterna of segments one to eight are similar to their terga in size and shape. The cuticle is membraneous and bears on each segment a transverse row of small setae. The coriae are distinct. The ninth abdominal segment is longer than wide, slightly chitinized, and marked with a dark spot near the middle and on either side of the dorso-meson. The tergum is shield-shaped and provided with many dark colored setae. The lateral aspect of the segment appears to be glabrous. The sterna is shorter than the tergum, the cuticle is membraneous and armed with a transverse row of four small setae. The tenth abdominal segment is cylindrical, glabrous, directed caudo-ventrad and bears the large disk-like sucker.

Hyperaspini

The body is ovate and the first to the fourth abdominal segments are widest. The prothorax is wider than long and the caudal margin is longer than the cephalic. The ninth abdominal segment is directed ventrad, wider than long, the tergum very slightly chitinized and provided with a few small setae. The body is usually white or yellow in color. The larvae cover themselves with flocculent masses of wax-like excretion. The body is never provided with scoli, senti, strumae, or verrucae, but is usually armed with setae or small chalazae. In the early larval stages the epicranial suture is present, while in the adult larval stages the epicranial suture is wanting. The antennae are short, three-segmented, and slightly setaceous. The mandibles are provided with a slightly developed mola and the apex is never bifurcate.

Genera of Hyperaspini

Cephalic margin of the prothorax with setae about as long as the prothorax is wide and lateral tergal abdominal setae are about twice as long as the segments bearing them.....*Brachyacantha*

Cephalic margin of the prothorax with setae which are not as long as the prothorax is wide and the lateral tergal abdominal setae are shorter than the segments bearing them.....*Hyperaspis*

Brachyacantha Chevrolat

This genus is represented by a single species.

Brachyacantha ursina Fab.—The dorsal portion of the head is slightly chitinized. The head is light yellow in color; the mouth is directed ventrad and slightly cephalad. The body is elongate, widest at the second and third abdominal segments, white to light-cream-colored, usually covered with a flocculent wax-like excretion. The prothorax is one-half as long as wide. The dorsal shield is wanting, but the cephalic margin of the prothorax bears eight setae which are longer than the segment is wide, the lateral margin bears two setae which are also longer than the segment. The lateral aspect is poorly defined and glabrous; the sternum is small and without setae. The mesothorax and metathorax are each about three times as wide as long, are provided with a seta near the lateral margin which is longer than the segment, and the lateral aspects are not well defined. The mesothoracic spiracles are located in the mesocoria near the cephalic margin of the segment, the metathoracic spiracle is wanting or rudimentary. The legs are short and not well developed, rarely extending beyond the sides of the body. Abdominal segments one to eight are similar. The terga are strongly convex, the dorsal and dorso-lateral setae are longer than the segments bearing them, and the spiracles are located near the cephalo-ventral margin of each tergum. The lateral aspect of each segment is provided with two large setae which are not longer than

the segments bearing them, the lateral setae are larger than the paralateral ones. The sterna are flat; each, except the first, bears a transverse row of four large setae. In the first segment the ventro-lateral setae are wanting. The caudal margins of the seventh and eighth sterna are deeply emarginate. The tergum of the ninth segment is semicircular, about as wide as long, and the dorsal surface is densely setaceous. The ninth sternum is small and bears four small setae. The tenth segment is small, cylindrical, glabrous, and directed ventrad.

Hyperaspis Redtenbacher

The members of this genus are generally white to cream-colored, and the body is usually covered with a flocculent wax-like mass. When seen from the dorsal aspect, the body is oval to elongate in outline, the dorsum is strongly convex and the sternum is more or less flattened. The prothorax is wider than long and bears setae which are not as long as the prothorax is wide. The ninth abdominal segment is semicircular, wider than long, and usually retracted into the eighth segment. The legs are small, short, and well developed. The mandibles are unidentate and serve as piercing organs. The members of this genus are carnivouous living for the most part upon aphids and soft-bodied coccids.

Species of Hyperaspis

Body elongate-ovoid and densely covered with dark hair-like setae ..... *H. binotata*

Body oval, not elongate, apparently glabrous, but with a few small inconspicuous setae ..... *H. signata*

Hyperaspis binotata Say.—The dorsal aspect of the body is brownish-yellow to yellowish-gray; the front, vertex, and clypeus are spotted with light or dark brown areas and provided with numerous setae. The prothorax is about twice as wide as long and the cephalic and lateral margins bear setae as long as the segment. The mesothorax and metathorax are subequal in length, but the latter is the wider. The lateral margin of the mesothorax is provided with a group of setae about as long as the segment, while the lateral margin of the metathorax has a distinct chalaza on each side which is surrounded by a group of long setae. The lateral margins of abdominal segments one to eight are each provided with a chalaza surrounded by a distinct group of setae. The dorsal surface of the thoracic and abdominal segments are densely covered with short black setae. The sterna and lateral aspects of the entire larva are provided with numerous fine and inconspicuous setae. The tergum of the ninth abdominal segment is about twice as wide as long, not strongly chitinized, and the caudal and lateral margins bear setae which are longer than the segment. The sternum is about one-half as long as the tergum and deeply emarginate on

the caudal margin. The tenth segment is small, cylindrical, and slightly chitinized, with a few fine setae on its surfaces. The segment is usually directed caudo-ventrad. The rectum has been evaginated to form a sucking disk. The legs are short and well developed, but do not extend beyond the sides of the abdomen in the adult larvae. The coxacoriae are distant.

Hyperaspis signata Oliv.—The general form of the body is oval, the dorsal surface is globose. The body is usually light-yellow to yellowish-green in color. The dorsal aspect of the head is brown, tan, or yellowish gray. The cephalic portions are spotted with small brown or black areas. The head is provided with many setae which are usually the longest setae found on the entire body. The tergum of the prothorax is rectangular and about twice as wide as long. The dorsal shield is wanting and the lateral and caudal surfaces are provided with setae which are about as long as the segment. The mesothorax and metathorax are subequal in length, but the metathorax is wider than the mesothorax. The lateral margins of both of these segments are provided with a few short setae which are not as long as the segment. The dorsal aspect of abdominal segments one to eight are similar and strongly convex, with a very distinct coria between the segments, and never densely setaceous but provided with a few setae which are never as long as the segment bearing them. The lateral margin of the dorsal aspect of the abdomen is provided with a series of lobes between the annulets. These lobes are provided with a few setae which are not as long as the segment. The sterna and the lateral aspect of segments one to eight are provided with a few short setae which are almost invisible. The tergum of the ninth abdominal segment is more or less shield-shaped, more than twice as wide as long, with the caudal margin broadly rounded. The lateral and caudal margins bear setae which are not as long as the segment. The ninth sternum is about one-half as long as the tergum, its cephalic margin is broadly convex while the caudal margin is deeply emarginate. The sternum and the lateral aspects are provided with a few small setae. The tenth abdominal segment is retracted into the ninth so that, as a rule, it is not visible. The tenth segment is small, circular, and membraneous. The rectum is evaginated to form a sucking disk. The legs are small, dark brown, and well developed, but do not extend beyond the sides of the body.

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PLATE I

EXPLANATION OF PLATE

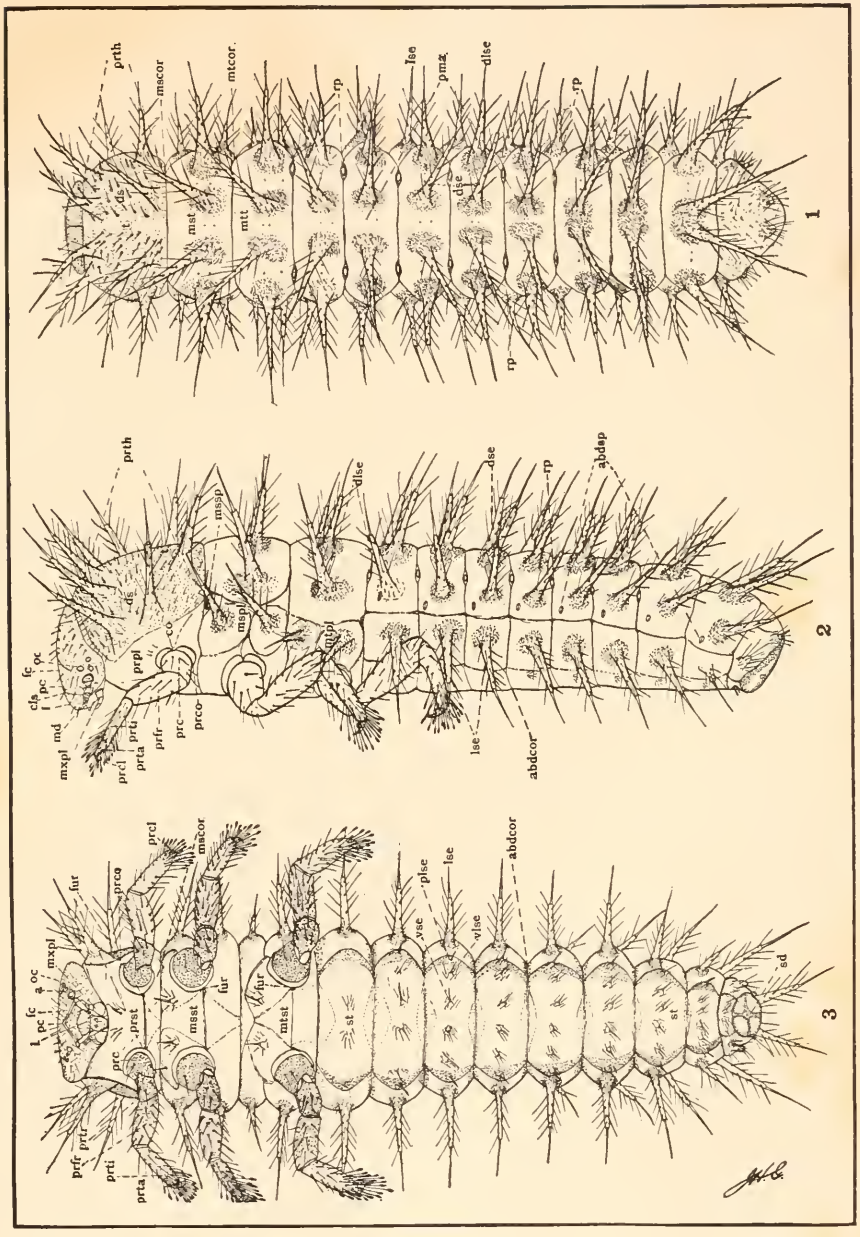
CHILOCORUS BIVULNERUS

Fig. 1. Larva, dorsal aspect.

Fig. 2. Larva, lateral aspect.

Fig. 3. Larva, ventral aspect.

abdcor	abdominal coria
abdsp	abdominal spiracle
cls	clypeo-labral suture
co	coxacoria
dse	dorsal senti group
dlse	dorso-lateral senti group
ds	dorsal shield
fc	front and postclypeus
fur	furcinia
l	labrum
lse	lateral senti group
md	mandible
mscor	mesocoria
mspl	mesopleural area
msst	mesosternum
mssp	mesothoracic spiracle
mst	mesotergum
mtcor	metacoria
mtpl	metapleural area
mtst	metasternum
mtt	metatergum
mxpl	maxillary palpus
oc	ocelli
pc	preclypeus
plse	paralateral senti group
pma	points of muscle attachment
prc	procoxa
prco	procoxacoria
prcl	protarsal claw
prfr	profemur
prpl	propleural area
prst	prosternum
prta	protarsus
prti	protibia
prth	prothorax
prtr	protrochanter
rp	repugnatorial pore
sd	sucking disk
st	sternum
t	tergum
vlse	ventro-lateral senti group
vse	ventral senti group



GAGE LARVAE OF THE COCCINELLIDAE PLATE I

PLATE II

EXPLANATION OF PLATE

CEPHALIC ASPECT OF THE HEAD

Fig. 4. *Epilachna borealis.*
Fig. 5. *Chilocorus bivulnerus*, lateral aspect.
Fig. 6. *Chilocorus bivulnerus.*
The label *cls* for the clypso-labral suture is wanting.
Fig. 7. *Megilla maculata.*
Fig. 8. *Hippodamia 13-punctata.*
Fig. 9. *Hippodamia convergens.*

a	antenna
cls	clypeo-labral suture
cs	clypeal suture
ea	epicranial arms
es	epicranial stem
fc	front and clypeus
ga	galea
ge	gena
l	labrum
lipl	labial palpus
md	mandible
mco	mandacoria
mxpl	maxillary palpus
oc	ocelli
pc	preclypeus
pcl	precolia
pf	palpifer
pt	pretentorina
ss+ca	fused stipes and cardo
supt	supratentorina
v	vertex

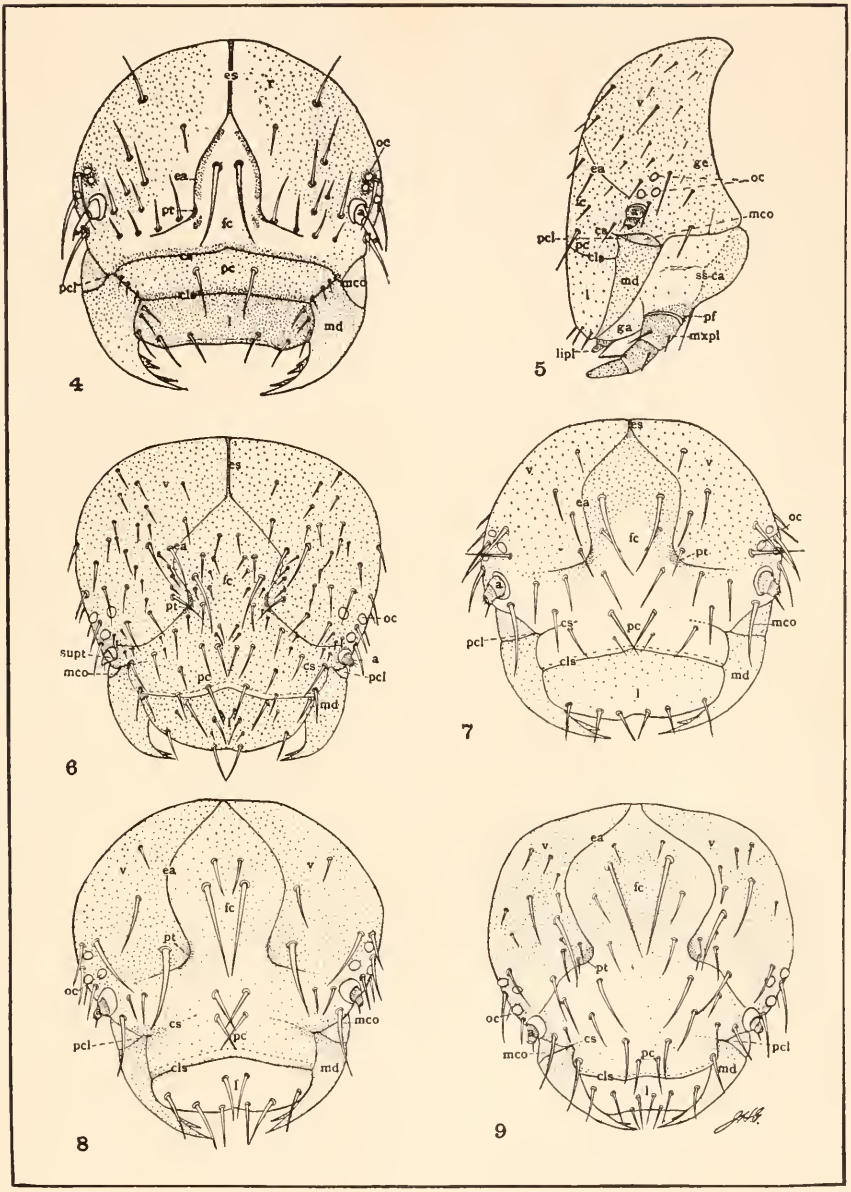

es
oc
ea
pt
fc
cs
pc
pcl
cls
mco
md
4
v
ge
ss-ca
pf
mxpl
lipt
ga
5
supt
a
6
7
8
9

PLATE III

EXPLANATION OF PLATE

CEPHALIC ASPECT OF THE HEAD

Fig. 10. *Coccinella 9-notata.*

Fig. 11. *Anatis 15-punctata.*

Fig. 12. *Adalia bipunctata.*

Fig. 13. *Microweisea misella.*

Fig. 14. *Scymnus* sp.

Fig. 15. *Hyperaspis binotata.*

a	antenna	*mc*	mandacoria
cls	clypeo-labral suture	*oc*	ocelli
cs	clypeal suture	*pc*	preclypeus
ea	epicranial arms	*pcl*	precoila
fc	front and postclypeus	*pt*	pretentorina
fc+v	front, postclypeus and vertex	*v*	vertex
l	labrum		
md	mandible		

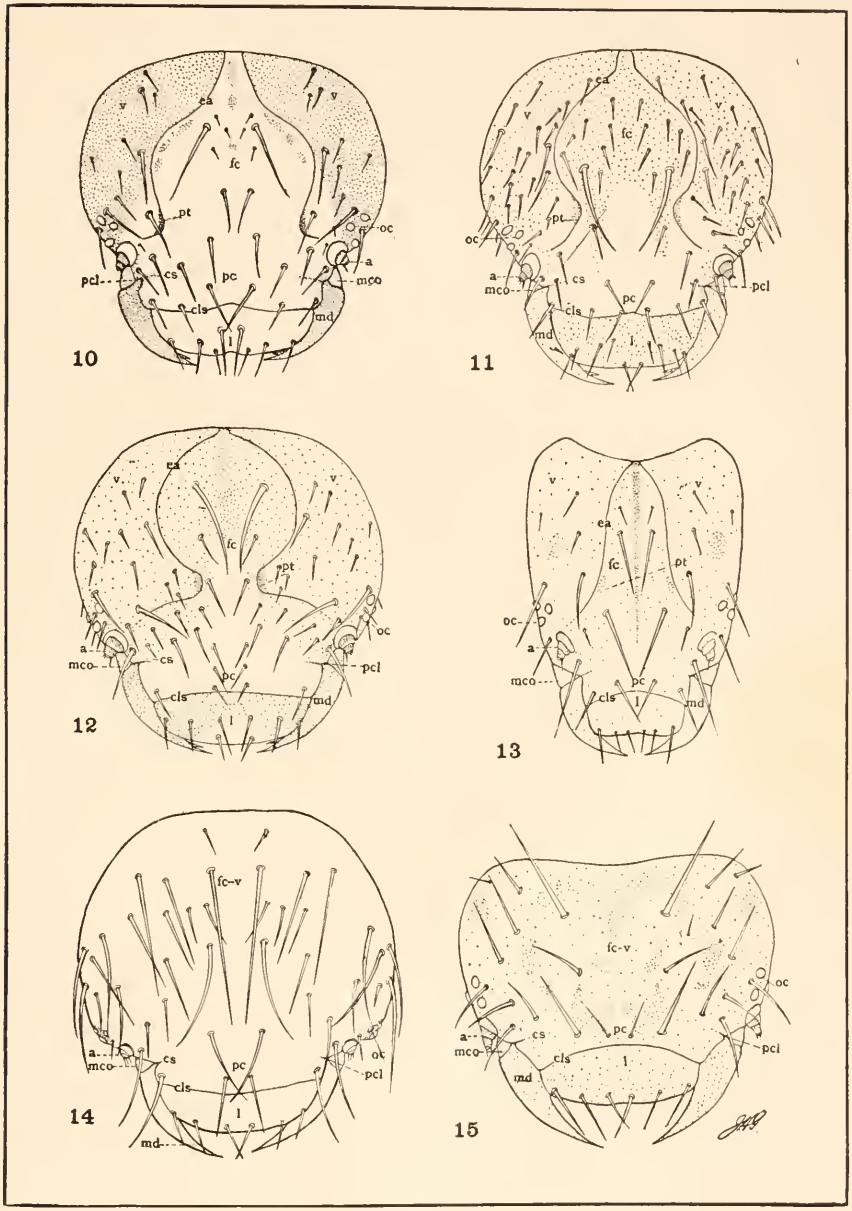

10
v
ea
fc
pt
oc
pcl
cs
pc
a
mco
cls
md
l
11
12
13
14
fc-v
15

PLATE IV

EXPLANATION OF PLATE

VENTRAL ASPECT OF THE HEAD

Fig. 16. *Epilachna borealis.*
The Label *Pg* for the palpiger is wanting.

Fig. 17. *Chilocorus bivulnerus*, caudal aspect.

Fig. 18. *Chilocorus bivulnerus.*

Fig. 19. *Megilla maculata.*
The Label *su* for the submentum is wanting.

Fig. 20. *Hippodamia 13-punctata.*
The Label *lig* for ligula is wanting.

Fig. 21. *Hippodamia convergens.*

cb chitinous band
cp corpotentorium
ea epicranial arms
es epicranial suture
g gula
ga galea
ge gena
lic labiacoria
lig ligula
lipl labial palpus
mxc maxacoria
mxpl maxillary palpus
of occipital foramen
pf palpifer
pg palpiger
pt pretentorina
ss + *ca* fused stipes and cardo
su submentum
sup supratentorium
ts tactile setae

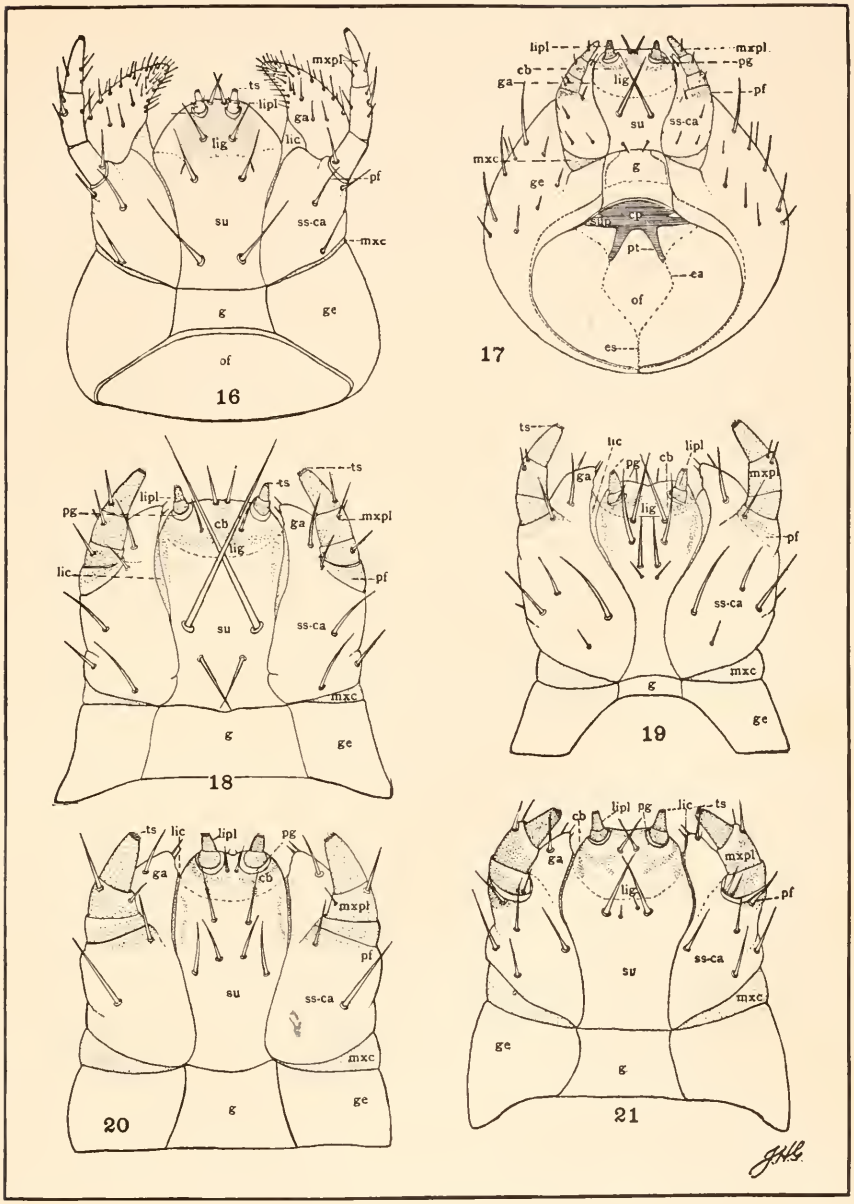

mxpl
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mxc
g
ge
20
cb
lipl
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PLATE V

EXPLANATION OF PLATE

VENTRAL ASPECT OF THE HEAD

Fig. 22. *Coccinella 9-notata.*

Fig. 23. *Anatis 15-punctata.*

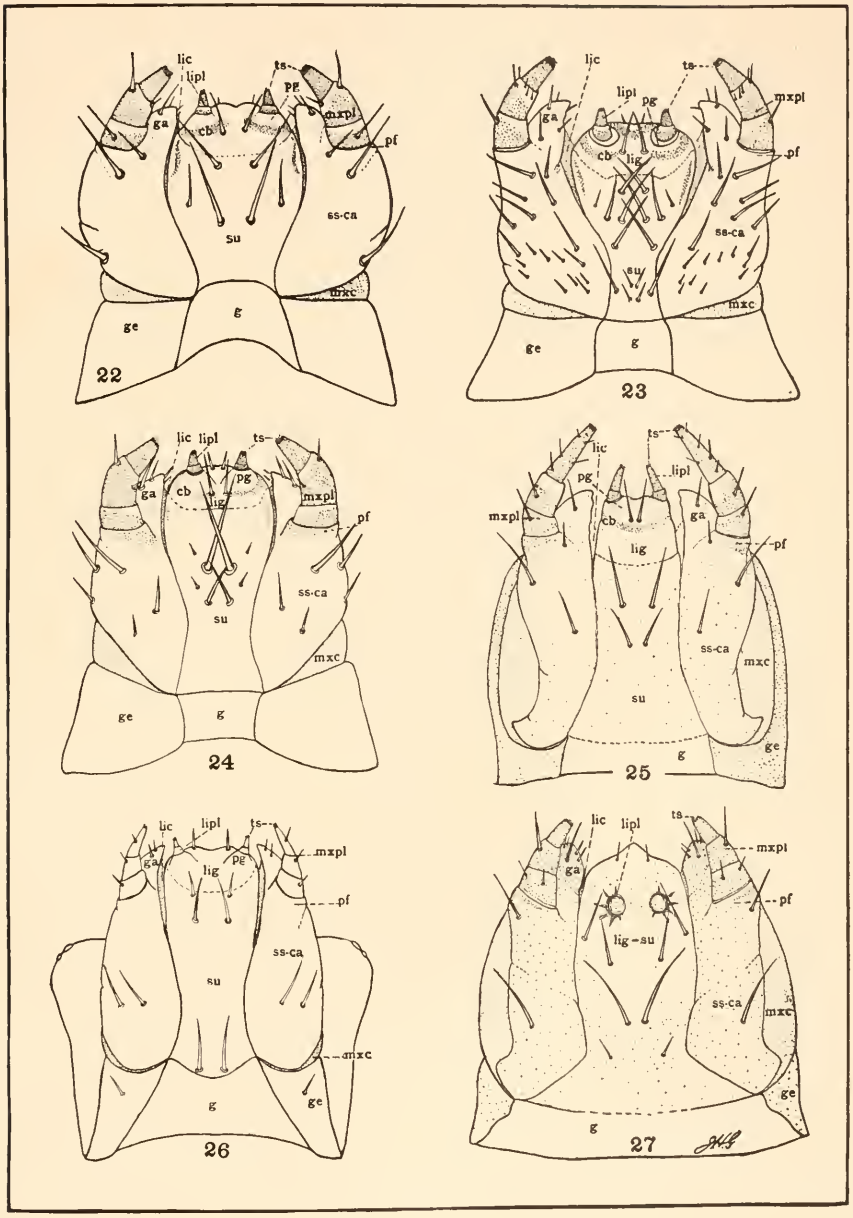
Fig. 24. *Adalia bipunctata.*

Fig. 25. *Microweisea misella.*

Fig. 26. *Scymnus* sp.

Fig. 27. *Hyperaspis binotata.*

cb	chitinous band	mxc	maxacoria
g	gula	*mxpl*	maxillary palpus
ga	galea	*pf*	palpifer
ge	gena	*pg*	palpiger
lic	labiacoria	*ss+ca*	fused stipes and cardo
lig	ligula	*su*	submentum
lipl	labial palpus	*ts*	tactile setae



GAGE LARVAE OF THE COCCINELLIDAE PLATE V

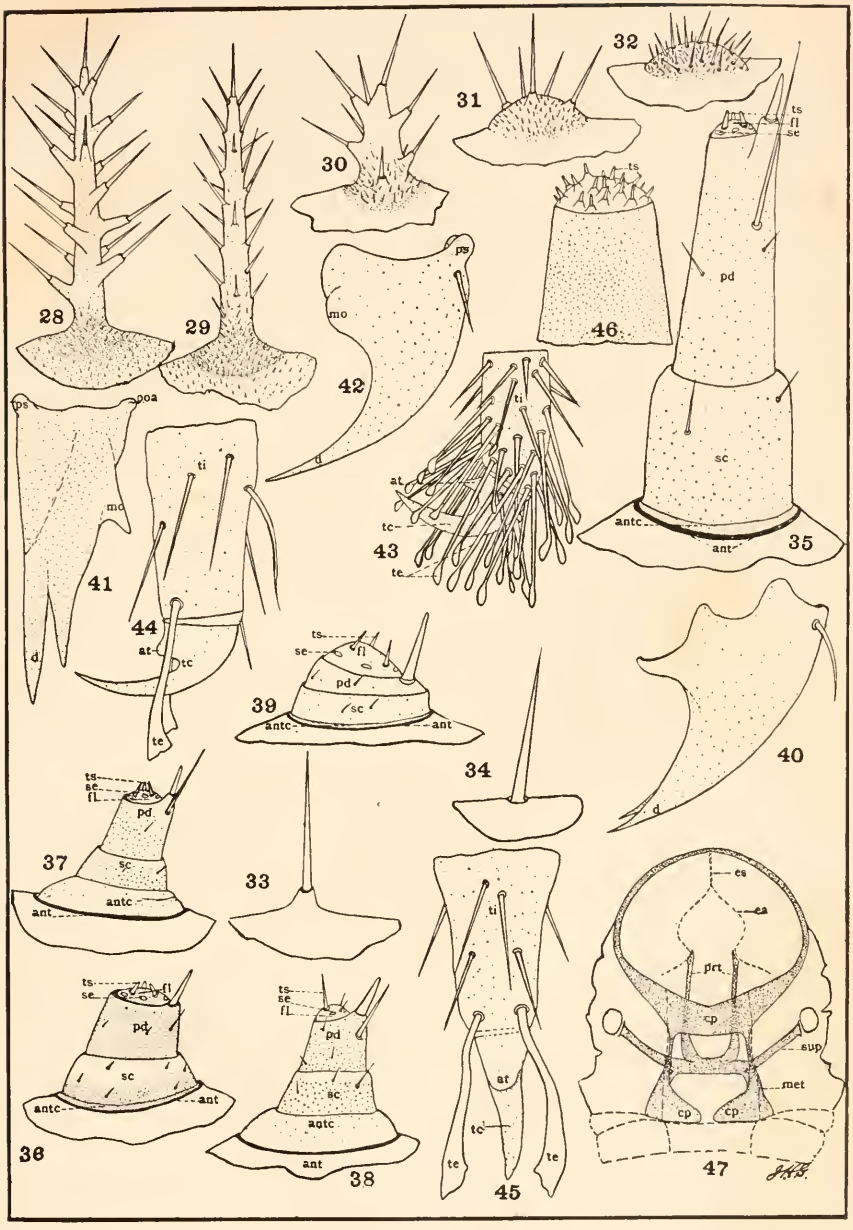
PLATE VI

EXPLANATION OF PLATE

MISCELLANEOUS PARTS OF THE BODY

Fig. 28. Scolus, *Epilachna borealis.*
Fig. 29. Sentus, *Chilocorus bivulnerus.*
Fig. 30. Parascolus, *Hippodamia convergens.*
Fig. 31. Struma, *Megilla maculata.*
Fig. 32. Verruca, *Microweisea misella.*
Fig. 33. Chalaza, *Hippodamia convergens.*
Fig. 34. Seta, *Hyperaspis binotata.*
Fig. 35. Antenna, *Epilachna borealis.*
Fig. 36. Antenna, *Chilocorus bivulnerus.*
Fig. 37. Antenna, *Hippodamia convergens.*
Fig. 38. Antenna, *Hyperaspis binotata.*
Fig. 39. Antenna, *Scymnus* sp.
Fig. 40. Mandible, *Chilocorus bivulnerus*, lateral aspect.
Fig. 41. Mandible, *Chilocorus bivulnerus*, mesal aspect.
Fig. 42. Mandible, *Microweisea misella.*
Fig. 43. Tarsus, *Chilocorus bivulnerus.*
Fig. 44. Tarsus, *Microweisea misella*, lateral aspect.
Fig. 45. Tarsus, *Microweisea misella*, ventral aspect.
Fig. 46. Tip of labial palpus, *Chilocorus bivulnerus.*
Fig. 47. Tentorium, *Chilocorus bivulnerus.*

ant	antennaria
antc	antacoria
at	appendiculated tooth
cp	corpotentorium
ea	epicranial arms
es	epicranial stem
d	dentes
fl	flagellum
met	metatentoria
mo	mola
pd	pedicel
poa	postartis
prt	pretentorium
ps	preartis
sc	scape
se	sensoria
sup	supratentorium
tc	tarsal claw
te	tenent hair
ti	tibia
ts	tactile setae



GAGE LARVAE OF THE COCCINELLIDAE PLATE VI